Improving the apple carbon balance model MaluSim by integrating and testing water deficit and fruit drop effects

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ZUSAMMENFASSUNG

Der Apfel ist eine der wichtigsten kommerziell angebauten Obstarten in Deutschland. Für die Apfelproduzenten gibt es jedoch einige Methoden und Investitionen, die mit großen Unsicherheiten behaftet sind. Die Ausdünnung wird schon seit vielen Jahren eingesetzt und ist eine essentielle Methode für den erfolgreichen Apfelanbau. Jedoch zeigt sie eine sehr hohe Variabilität zwischen Jahren als auch zu verschiedenen Zeitpunkten innerhalb eines Jahres und liefert dadurch häufig unerwartete Ergebnisse. Außerdem beschäftigt die Anbauer die Frage ob aufgrund des fortschreitenden Klimawandels eine Zusatzbewässerung vor allem für die Etablierung von jungen Bäumen mit noch geringem Wurzelvolumen in Zukunft notwendig sein wird. Um diese wichtigen Entscheidungen in Zukunft erleichtern zu können wurde im Rahmen dieser Arbeit ein universell einsetzbares Apfel-Modell zur Anwendung in Deutschland und Mitteleuropa erarbeitet. Als Basis diente das in den USA entwickelte Kohlenstoffbilanzmodell MaluSim. Dieses wurde zunächst an mitteleuropäische Bedingungen angepasst und erste Simulationsläufe zum Vergleich mit dem Originalmodell wurden durchgeführt. Hierbei zeigte die Simulation der kumulierten Gesamt-Assimilatproduktion einer Saison bei den, nur ein Drittel so großen, deutschen Standardbäumen halb so hohe Werte als für Standardbäume in den USA.

Im Folgenden wurde das bisher nicht funktionierende MaluSim Fruchtsubmodell modifiziert und dahingehend getestet, ob es in der Lage ist, den natürlichen Fruchtfall korrekt zu berechnen. Hierfür wurden modellierte Fruchtzahlen mit gezählten Fruchtzahlen unausgedünnter Varianten von Apfelanlagen aus Versuchen in Zornheim (D), Jork (D), Lindau (CH), Güttingen (CH) und Wädenswil (CH), verglichen. Bei diesem Test konnte das modifizierte Modell ‘G4-4’ besonders überzeugen. Die mittlere Abweichung der modellierten Werte zu den tatsächlich gezählten Fruchtanzahlen lag bei lediglich 3,7 %. Die Ergebnisse zeigen, dass das modifizierte Modell ‘G4-4’ den natürlichen Fruchtfall sehr zufriedenstellend berechnen konnte und dass das Modell das Potential hat auch im Bereich Ausdünnungsempfehlungen eingesetzt zu werden.

Des Weiteren wurde, basierend auf veröffentlichten Daten, ein Wassersubmodell entwickelt und in das Modell ‚G4-4‘ integriert. Hierbei wurde das mittägliche Stammwasserpotential als Indikator für den Wasserstatus des Baumes herangezogen. Aus diesem Parameter werden Wasserdefiziteffekte für das Langtriebwachstum, die Respiration, sowie für die Photosynthese berechnet. Erste Simulationsläufe zeigen generell realistische, mit veröffentlichten Erkenntnissen vergleichbare, Ergebnisse. Das Submodell ermöglicht eine Simulation von unterschiedlich starken Wasserdefiziteffekten zu variablen Zeitpunkten.

Zusätzlich wurde zur Untersuchung der Auswirkungen von Zusatzbewässerung und Wassermangel auf neugepflanzte Apfelbäume ein Feldexperiment in Geisenheim, Deutschland durchgeführt. Jungpflanzen der Sorten ‘Fresco’ (‘Wellant®’), ‘Jugala’, und ‘AW 106’ (‘Sapora®’) wurden im Herbst 2011 in randomisierten Blöcken gepflanzt. Ab 2012 erfolgten drei verschiedene Bewässerungsvarianten: CT (Kontroll-Behandlung) wurde nicht bewässert und nur durch natürliche Regenfälle befeuchtet, NT (Normal-Behandlung) wurde zusätzlich mit 2 l/Baum/Tag bewässert, und ET (Evapotranspiration-Behandlung) wurde nach Berechnung der Wasserbilanz (Niederschlag und Verdunstung) bewässert. Die Auswirkungen der drei Varianten auf das Wachstum und die Physiologie der Bäume wurden in den Jahren 2012 und 2013 gemessen. Neben Bodenwassergehalten wurde der Wasserstatus der Bäume durch die Messung des frühmorgendlichen sowie des mittäglichen Stammwasserpotentials bestimmt.

In beiden Versuchsjahren kam es zu höheren Niederschlagsmengen als im 30-jährigen Mittel von 1981 bis 2010, wobei 2013 nasser als 2012 war. Statistisch signifikante Unterschiede zwischen den Varianten konnten vor allem in der Saison 2012 gefunden werden. 2012 war das vegetative Wachstum der Bäume in den beiden bewässerten Varianten NT und ET bei allen Sorten signifikant höher als in der unbewässerten CT Variante. In der niederschlagsreicheren Saison 2013 zeigten sich ähnliche Tendenzen, jedoch konnten nur bei ‚Jugala‘ und ‘Fresco’ signifikante behandlungsbedingte Unterschiede des Langtriebwachstums und der Holzoberfläche nachgewiesen werden, während für ‘AW 106’ die Unterschiede im Langtriebwachstum nicht statistisch signifikant waren. Ähnliche Ergebnisse zeigten sich für die erste Ernte in 2013. Die Lichtaufnahme, sowie die berechnete Gesamtblattfläche, der Bäume, gemessen für ‘Fresco’, war in beiden Jahren statistisch signifikant deutlich niedriger in der unbewässerten CT Variante (2012: 17,4 %; 2013: 24,9 %) als bei ET (2012: 26,3 %; 2013: 42,1 %) und NT (2012: 24,2 %; 2013: 38,3 %). Des Weiteren konnten zu bestimmten Zeitpunkten signifikant niedrigere Photosyntheseraten für CT als für ET und NT durch Gaswechselmessungen der Blätter nachgewiesen werden. Durch eine Gruppierung der Werte in Bezug auf das zugehörige gemessene mittägliche Stammwasserpotential der Bäume konnte belegt werden, dass mit abnehmendem Wasserpotential auch die Photosyntheserate statistisch signifikant abnimmt. Der Beginn des Absinkens liegt im Bereich zwischen -1 und -1,5 MPa.

Die Ergebnisse des Versuchs zeigen, dass, trotz der höheren Niederschlagsmengen, die Zusatzbewässerung einen ausgesprochen positiven Effekt auf die Etablierung der Bäume hatte. Dieser Effekt sollte in trockenen Jahren noch deutlich ausgeprägter ausfallen.

ABSTRACT

Apple (*Malus x domestica* Borkh.) is the major tree fruit in Germany, but there still exist major uncertainties in commercial apple production. Thinning has been practiced for many years and is an essential part for successful apple production, but is still an unpredictable part with large variations from year to year and even within years. Another uncertainty for apple growers is the need of apple trees for adequate water supply. Due to the advancing climate change apple growers are uncertain whether additional irrigation will be necessary during the establishment phase of young apple trees.

Therefore, to facilitate these decisions in future, the motivation of this study was to acquire a universal apple model to be used in Germany and Central-Europe. The apple carbon-balance model MaluSim which has been developed in the USA was chosen as a basis. At first, the model has been parameterized for German growing conditions and first simulation runs were conducted. In comparison to the original model, the seasonal assimilate production for German standard trees was about half of the one for standard trees in the USA, while standard trees in Germany were only about one third of the size of US ones.

Subsequently, the previously untested fruit growth and abscission submodel has been modified and tested. Simulated final fruit numbers were compared to counted fruit numbers of unthinned trials in Zornheim (GER), Jork (GER), Lindau (CH), Güttingen (CH) and Wädenswil (CH). The modification 'G4-4' showed good simulation results with very low deviations to actual fruit numbers. Average deviation to fruit numbers was only 3.7 %. Results indicate that the model is able to very adequately calculate final fruit numbers of natural fruit drop of Central-European apple trees and that it could be a tool used for thinning advices.

Based on published data, a new water submodel has been included into the MaluSim framework to additionally improve the model. Midday stem water potential has been used as an indicator for water status of the tree. A water stress effect on long shoot growth, respiration, and photosynthesis based on midday stem water potential was used in the water submodel. First simulation runs using the new water submodel indicate that general behavior is realistic. Modeling results generally corresponded to findings of published experimental results. The submodel is able to simulate variable intensities of water deficit effects at variable times.

To study the effects of additional irrigation and water deficits on young apple orchards a field experiment was conducted during 2012 and 2013 in Geisenheim, Germany. Trees of the cultivars ‘Fresco’ (‘Wellant®’), ‘Jugala’, and ‘AW 106’ (‘Sapora®’) were planted in autumn 2011 in a randomized plot design. In 2012, three irrigation treatments, CT (control treatment, only rain fed), NT (normal treatment, irrigated with 2 L/tree/day), and ET (evapotranspiration treatment, irrigation based on calculated water balance), were applied and effects on tree growth and physiology were recorded in 2012 and 2013. Besides soil moisture, water status of the trees has been recorded using predawn and midday stem water potential measurements.

In both years, amounts of precipitation were higher than the 30-year average for the site, with 2013 being wetter than 2012. Between treatments, statistically significant differences developed in both seasons, but were less profound in 2013. In 2012, vegetative growth recorded in NT and ET was statistically significantly higher than in CT for all cultivars. In the wetter season 2013, similar tendencies evolved. But only in ‘Jugala’ and ‘Fresco’ long shoot growth and wood surface area was significantly higher, while for ‘AW 106’ differences in long shoot growth were not statistically significant. Similar results were obtained for the first harvest in 2013.

Light interception and calculated leaf area, measured in ‘Fresco’, was significantly lower in CT trees (2012: 17.4 %; 2013: 24.9 %) compared to ET (2012: 26.3 %; 2013: 42.1 %) and NT (2012: 24.2 %; 2013: 38.3 %), in both years. Additionally, differences between CT and the two irrigated treatments were found for leaf gas exchange rates during the seasons. A relationship between midday stem water potential and leaf gas exchange has been confirmed. Grouping of photosynthesis measurements according to midday stem water potentials led to statistically significant differences between groups. Photosynthesis started to decrease between -1 and -1.5 MPa.

In conclusion, the results show that although both years have even been wetter than usual, the additional irrigation was highly beneficial for tree growth and had a positive effect on orchard establishment. This effect is supposed to be considerably higher in drier years.

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LIST OF ABBREVIATIONS

ABA	abscisic acid
ANOVA	analysis of variance
a_r	respiration rate at $T = 0$ °C
$Carbon_{avail}$	available carbon
$\mathrm{C_i}$	intercellular CO_2 concentration
CT	control treatment
DegDay	degree day using a base temperature of 4 °C
$Demand_I$	carbon demand of a given organ
$Demand_{total}$	total demand for carbon
DI	deficit irrigation
DOY	day of year
e.g.	for example (exempli gratia)
ET	evapotranspiration treatment
et al.	and othera (et alia)
$\mathrm{ET_C}$	crop specific evapotranspiration
$\mathrm{ET_O}$	reference evapotranspiration
FDR	frequency domain reflectometry
F_{max}	fractional light interception if trees were opaque
FSM	functional structural model
GM	geometrical model
$\mathrm{g_s}$	stomatal conductance
h	day length in seconds
k	canopy light extinction coefficient
$\mathrm{k_c}$	crop coefficient for evapotranspiration calculation
k_r	temperature coefficient of R
L	liter
LA_{incr}	calculated leaf area increment per shoot per day
LAI	leaf area index
LI	light interception
LRC	light response curve
NT	normal treatment
PAR	photosynthetically active radiation
PBM	process based model
P_{daily}	daily gross photosynthetic rate
P_{max}	rate of light saturated leaf photosynthesis
Pn	net photosynthetic rate
PN1750	net photosynthetic rate at a light intensity of 1750 μmol m^{-2} s^{-1}
PPF	photosynthetic photon flux
PPFD	photosynthetic photon flux density
PRD	partial rootzone drying
R	respiration rate
RDI	regulated deficit irrigation
RP_i	relative partitioning to a given organ
RSS	relative sink strength
RSS_i	relative sink strength of a given organ
S	daily integral of total radiation on a horizontal surface
T	temperature in °C
$\mathrm{T_c}$	light transmitted to the ground by passing through the canopy
TDR	time domain reflectometry
$\mathrm{T_f}$	light transmitted to the floor between the trees
VPD	vapor pressure deficit
WUE	water use efficiency
α	leaf photochemical efficiency
Ψ_{stem}	midday stem water potential
Ψ_{pd}	predawn water potential

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1 GENERAL INTRODUCTION

The domesticated apple (*Malus* x *domestica* Borkh.) is one of the most important fruit crops in Europe. In Germany, the most important apple growing regions are the 'Altes Land' in the North, and the area surrounding Lake Constance in the South of Germany. Total production area is around 32000 ha, with an average total production of about 950000 tons per year (FAOSTAT, 2015). Consumers and the apple industry have high requirements on the inner and outer quality of apple fruits (NEMESKÉRI, 2007) and expect specific fruit sizes.

In the past, apple growers in Germany were able to produce high quality apples without the need to use any irrigation in their orchards due to sufficient rain events and amounts during the season. But with the changing climate uncertainty of the growers increases whether additional irrigation will be an essential requirement for high quality production in the future (STÖCKLE et al., 2011). Although the total precipitation amount per year is not supposed to change much, it is expected that the distribution of rain events will change and longer drought periods may occur (ZEBISCH et al., 2005) during the growing season. Water is one of the major factors for the determination of fruit size and total yield (JONES et al., 1985). Longer periods with no rain and therefore arising drought affects fruit development and number, and reduces tree growth (LANDSBERG & JONES, 1981; MILLS et al., 1996).

A good water supply during the first years of orchard development guarantees a good development of the trees and can lead to earlier and higher yields and thus an earlier return of investment. But the use of additional irrigation also means higher investments for the farmers with unclear payout (BRAVIN et al., 2008). To add sufficient water for the trees, but also to use as little water as possible to save water and costs, makes irrigation scheduling a very difficult task (NEILSEN & NEILSEN, 2002; NAOR & COHEN, 2003; FALLAHI et al., 2006; CASADESUS et al., 2011). In water-limited regions around the world it is already essential to use as little water as possible by still producing high quality fruits and yields (BEHBOUDIAN et al., 2011). This shows that knowledge about the water relations of apple trees is a very important topic for Germany, but also for other apple growing regions around the world.

Another main cultural practice in apple production to ensure a good and marketable fruit size is thinning. Usually less than 10 % of the initial flowers are needed for high quality yields, which makes thinning essential. Method and timing of thinning can have an enormous effect on this year's and also on next year's apple production (LINK, 2000; BYERS & CARBAUGH, 2002; GREENE, 2002; SCHRÖDER & BANGERTH, 2006) by preventing 'biennial bearing' (TROMP, 2000).

Several phases of natural flower or fruit drop can be observed during apple development (BERÜTER & DROZ, 1991), which makes the task of artificial thinning even more complicated. The worst case for growers is overthinning. They earn less money due to the lower total amount of apples and due to the oversized and thus lower quality apples. But also insufficient thinning is not beneficial for successful commercial apple production and the consequences depend on the degree of underthinning. It usually means lower potential fruit size and much higher hand thinning costs, but it can additionally reduce next year's flower numbers thereby inducing biennial bearing. Many environmental and tree internal factors have an effect on natural fruit drop and on thinning efficiency. Although thinning is used in apples since over 50 years (WERTHEIM, 2000), and hundreds of experiments were conducted with diverse ways of thinning (LINK, 1978; BYERS et al., 1990a; WERTHEIM, 2000; GREENE, 2002; PFEIFFER & RUEß, 2002; ZIBORDI et al., 2009; SOLOMAKHIN & BLANKE, 2010), there are still gaps in the understanding, and large uncertainties for the growers remain.

Models can be used to summarize knowledge and to increase the understanding of real world phenomena (LENTZ, 1998). They offer powerful tools to identify and understand the main factors influencing a cropping system. Therefore the uncertainties of today's apple production, in particular thinning activities, might be reduced by using models. In addition, models can be used to approach future problems related to irrigation and water deficits in apples. This may for example help to answer whether additional irrigation is reasonable at a specific site or not.

2 LITERATURE REVIEW

2.1 An introduction to modeling

Biological systems are very complex and one can rarely achieve a complete mathematical description of their behavior (JONES, 2014a). Therefore, a model is an attempt to describe a certain process or system through the use of a simplified representation, which focuses on a few key variables that mainly control the process or system (GOLDSCHMIDT & LAKSO, 2005). Models can be classified in diverse ways. One for horticultural plant models is by their main use into one of two groups: 1. to improve our understanding (theoretical models) or 2. to provide management advices to growers (practical models). Scientifically, plant models are divided into three main classes: geometrical models, process-based models, and functional-structural models (DE REFFYE et al., 2008).

Geometrical models (GMs), or architectural models, try to simulate the 3-D architecture of plants. This may include the description of entire plants in isolation or within an ecological context, and also models of plant parts, like individual branches of shoot or root systems (PRUSINKIEWICZ, 2004). They are usually made out of empirical observations of real plants and can be used in landscaping, agronomy, or botany to obtain accurate organogenesis and realistic plant architecture (DE REFFYE et al., 2008). The most important principle belonging to this type of models is Lindenmayer-systems or L-systems (PRUSINKIEWICZ, 1997; based on LINDENMAYER, 1968). It takes advantage of the complexity of multicellular organisms by dividing modules into types. Examples for GMs are the ones of the group of COSTES for apricots (COSTES et al., 1992) or apples (COSTES & GUÉDON, 2002; RENTON et al., 2006). GMs are used to simulate plant architecture but not to assess plant biomass production and plant functioning and therefore are not suitable for the objectives of this thesis. For a detailed description of GMs see PRUSINKIEWICZ (2004), and PRUSINKIEWICZ & RUNIONS (2012).

The main aim of process-based models (PBMs) is to model plant functioning. Plants are considered only at the minimal level of organ compartments and no 3-D representation of the plant is produced (DE REFFYE et al., 2008). Plant organs of one category are often thought of as one big organ of this type, which is generally known as a 'big-leaf' approach. This greatly simplifies the modeling, but means that within-tree location of single organs cannot be taken into account (COSTES, 2004). Although the 3-D structure strongly affects processes inside a plant (e.g. carbon partitioning, light interception), the simplifications of PBMs can be sufficient and work well for many purposes. PBMs are mainly used to simulate crop production. This includes simulating dry matter production and its partitioning. Examples for fruit tree PBMs are one for apple, developed by SEEM et al. (1986), the MaluSim model by LAKSO et al. (see 2.2), or a kiwifruit model, developed by BUWALDA and co-workers (BUWALDA et al., 1990; BUWALDA, 1991; BUWALDA & MEEKINGS, 1992). A review of PBMs and their main components can be found in MARCELIS et al. (1998).

Functional structural models (FSMs) are very complex and try to imitate reality as closely as possible (DE REFFYE et al., 2008). They integrate relationships between plant structures and processes that underlie their growth and development (DEJONG et al., 2011). Hence, FSMs are a combination of GMs (structure) and PBMs (functioning). Many FSMs exist for annual plants, while only few are available for trees due to their perenniality and very high complexity. An important example for a tree FSM is L-PEACH (ALLEN et al., 2006; LOPEZ et al., 2008a; LOPEZ et al., 2008b; DA SILVA et al., 2011). Other examples are SIMWAL for walnut trees (BALANDIER et al., 2000), and for apple a RATP (radiation absorption, transpiration, photosynthesis) FSM (SINOQUET et al., 2001; MASSONNET et al., 2006) and MAppleT (COSTES et al., 2008; DA SILVA et al., 2014). FSMs might be able to provide new insights into the complex interactions among plant architecture, leaf physiology and the environment (MASSONNET et al., 2008; VOS et al., 2010). But complex models may require inputs that are not easy to obtain in a field situation (BOOTE et al., 1996), and most FSMs are highly theoretical and far from providing practical applications (DE REFFYE et al., 2008).

The term “carbon balance model” is often used in the literature. The use of computer simulation modeling has highlighted the importance of carbohydrate partitioning in determining crop growth and productivity (DEJONG & GROSSMAN, 1992). This type of model involves modeling of plant photosynthesis, respiration and the allocation of the assimilates to organs of interest (GOLDSCHMIDT & LAKSO, 2005) and can be either a PBM or a FSM.

So far, FSMs are mainly used for theoretical uses while PBMs are used for both, theoretical and practical uses. The MaluSim model is a PBM and has been used for theoretical and practical applications in the past with medium to good success (LAKSO et al., 1999; LAKSO et al., 2006a). It is a very promising model framework and therefore has been chosen as the basis for this thesis.

2.2 MaluSim

2.2.1 General

MaluSim is a carbon balance model for apple trees which has been developed and adjusted over many years by Alan N. Lakso and co-workers (LAKSO & JOHNSON, 1990; LAKSO et al., 1995; LAKSO et al., 1997; LAKSO et al., 1999; LAKSO et al., 2001b; LAKSO & NYROP, 2002; LAKSO et al., 2006a; LAKSO et al., 2006b; LAKSO et al., 2007; ROBINSON & LAKSO, 2011; LAKSO & ROBINSON, 2015). The original MaluSim model has been developed for the cultivar 'Empire' for Geneva, NY, USA, and the basic time step is one day (LAKSO & JOHNSON, 1990). It is a big-leaf model that also uses a 'big-leaf' simplification for other plant organs. For the development of MaluSim the auto-programming simulation software STELLA® was chosen, which makes it possible to use the model without the knowledge of specific computer programming skills and it reduces the time needed to run simulation tests (LAKSO & JOHNSON, 1990). In addition, it allows other fruit physiologists to easily work with and to extend the model.

2.2.1.1 Original objectives and possible uses

Some of the first objectives were to develop MaluSim as a model for apple so that fruit physiologists would be able to find general principles that control apple productivity, to integrate current data and to focus future research directions (LAKSO & JOHNSON, 1990). But over the years of its development more objectives and questions evolved and nowadays there exist different possible uses of MaluSim.

Because of the perennial nature and size of apples trees, classical growth analysis is very difficult and there is a need for useable models to address general questions. Thus one objective of the MaluSim model development was to compare effects of cultural practice and also to evaluate effects of environmental changes (LAKSO et al., 2006a). To be able to simulate growth under different environmental conditions has helped to understand why apple productivity varies in different climates and between years within the same climate (LAKSO et al., 2001b). Another main reason for the development of MaluSim was to determine periods in the season where carbon deficits and surpluses are likely to occur and how this affects orchard performance (LAKSO et al., 2006a). MaluSim indicates that the most likely time of carbon deficit is about two to three weeks after bloom. Another period of possible carbon deficit is at the end of the season, but the overall effect of late season limitations on the crop and tree is supposed to be much less than early deficits (LAKSO, 2011). An additional aim was to model the impact of short time effects on apple orchards. This includes for example effects of foliar pests on photosynthesis and thus on carbon balance. The authors simulated a European Red Mite infestation and compared model to experimental data with medium to good results (LAKSO & NYROP, 2002).

A more recent use of MaluSim is to help understand natural fruit drop and to give thinning advice. MaluSim calculates carbohydrate supply and demand balances. There are likely indications that carbon balance may be a baseline for chemical thinner responses (tree sensitivity to thinners), and the model may help to explain some of the year to year variations in natural fruit drop and in the effect of chemical thinning (LAKSO et al., 2006b; PARRA-QUEZADA et al., 2006). Model simulations from several years were able to show, that periods of particularly positive or negative carbon balance were associated with mild or severe chemical thinning responses, respectively (LAKSO & ROBINSON, 2015). By using weather forecasts the model has been used to provide real-time predictions of tree sensitivity to chemical thinning based on carbon relations (LAKSO et al., 2007; LAKSO & ROBINSON, 2015).

Obviously, MaluSim can not only be used for one single application. Over the years various questions were answered and it has been used to help understand different problems in diverse areas. Examples of the questions the MaluSim dynamic simulation model can address are: (1) what is the seasonal dry matter production and partitioning and integrals of carbon fluxes by photosynthesis and respiration of organs; (2) how do different climates or weather components (radiation, temperature) affect the growth and dry matter production; and (3) what are the seasonal patterns of carbon supply versus carbon demands, when are there likely excesses or deficits of carbon, and are these periods related to key performance or management issues. MaluSim has already been used to simulate and compare apple tree behavior at different sites (LAKSO et al., 2001b) which makes it appropriate for modeling of German apple trees.

2.2.1.2 General simplifications and limitations of MaluSim

Simplifications made in a complex system lead to the consequence that many limitations occur (LAKSO & JOHNSON, 1990). This includes for example processes which have not been modeled and assumptions or relationships that need improvement. A model is always a trade-off between accuracy, simplicity, usefulness especially by others, and intelligibility (GOLDSCHMIDT & LAKSO, 2005; ROUPSARD et al., 2008). MaluSim does not consider tree architecture (this includes for example leaf angle or position of fruits), which is a main disadvantage. But this also is one reason why it is possible to partly validate the model and to use it for practical purposes.

The plant is divided into plant organs (wood, roots, shoots, spurs, fruits), but no individual organ of one type is modeled. Each population of the same organ is treated as if it would be one big leaf (or the crop, the wooden structure, the canopy, the root system), which is called “big-leaf” simplification. For this it is assumed that, in matters of photosynthesis calculation, the total leaf area can be represented by a single layer that intercepts light (SPITTERS et al., 1986; DE PURY & FARQUHAR, 1997). The big-leaf approach assumes that the carbon flux of a single leaf has the same relative response to the environment as the whole canopy and that therefore scaling from the leaf to the canopy is linear (KULL & KRUIJT, 1999; FRIEND, 2001). Canopy photosynthesis is estimated as a daily canopy light response to daily intercepted radiation, which is based on incident radiation, fractional interception and exposed leaf photosynthesis. Gradients of light, photosynthesis of differing leaf populations, and varying geometry over time are ignored (GOLDSCHMIDT & LAKSO, 2005). Models using a big-leaf simplification are not able to consider or calculate canopy microclimate (RAUPACH & FINNIGAN, 1988) or effects of sunflecks and different leaf angles on absorbed radiation (DE PURY & FARQUHAR, 1997). Some big-leaf models use Beer’s law to calculate the absorbed irradiance of a canopy, which can lead to overestimation of canopy photosynthesis (SPITTERS et al., 1986; DE PURY & FARQUHAR, 1997; WANG & LEUNING, 1998). This problem is often solved by using empirical factors in the response of photosynthesis to irradiance. This kind of correction may not be independent of conditions and may reduce the accuracy of predictions at different conditions (DE PURY & FARQUHAR, 1997).

The use of big-leaf models extremely reduces the complexity of canopy photosynthesis modeling (DE PURY & FARQUHAR, 1997). This also has a positive effect on computing time and data requirements (RAUPACH & FINNIGAN, 1988; FRIEND, 2001). The number of required inputs is usually very low for big-leaf models. Although big-leaf simplifications have some shortcomings and are very simple, the simulated values can be quite good and satisfactory for their purposes (LAKSO & JOHNSON, 1990; AMTHOR, 1994; AMTHOR et al., 1994; LLOYD et al., 1995; DE PURY & FARQUHAR, 1997; GOLDSCHMIDT & LAKSO, 2005). Besides the big-leaf simplification, MaluSim uses a similar simplification for all plant organs (LAKSO, 2011). This simplification is then separated by the numbers of a particular organ, to simulate for example fruit growth and drop. The mean fruit weight is calculated, but not for a particular fruit and no distribution of fruit weights are modeled. For this reason it is not possible to model fruit quality with MaluSim.

Through the big-organ simplification some things are impossible to be modeled correctly, but it is sufficient for many uses (e.g. dry matter production), needs less data input, is faster to run, and is more comprehensible than more complex approaches. It is adequate to simulate an average apple tree and to get valuable tendencies of the orchard performance. However, all parts of MaluSim that deal with roots should be used with caution, because they are based on very limited data. Good studies of tree root parameters are very difficult and time consuming to conduct. Thus knowledge about tree roots is still very limited (see also chapter 2.4.4) and for the model confidence it is not useful to model relationships which have not been explored yet. Although modeling can be a good way to begin to examine such poorly known processes.

Another major limitation of MaluSim is that it only calculates the growing season and no carry-over effects are considered. Dormancy in winter is not included as well as the carry-over of reserves from one year to the next. One possible reason for this is that these effects are also not very well understood mechanistically and knowledge is still limited. Another reason might be that in most cases it is not very important for producers to know. Furthermore, apple orchards with no alternate bearing and good management usually stay very constant over the years and the standard tree calculation is appropriate. Additionally, the change of inputs like numbers of flowers is very easy and thus the model can be simply parameterized to some changes.

Some main factors affecting fruit set and development are not included in MaluSim. This includes for example effects of frost during flowering, or hormonal processes. Other factors, like pollination, hand thinning or pest damage, can be empirically entered by the user, but are not calculated by the model itself. When validating and evaluating MaluSim, one should keep in mind that it is not an objective to model one particular tree or every single tree of an orchard, but to give an idea of the general reactions of a particular orchard.

2.2.1.3 Required inputs

Like every model, MaluSim achieves best results when it is precisely parameterized to the site and prevailing conditions of interest. For practical applications that reflect only variations due to the environment, mature orchards are simulated and then MaluSim only has to be parameterized once and not every year again. This use is analogous to using the Penman-Monteith equation with set crop parameters to estimate the weather driven evapotranspiration. For research uses of MaluSim it can be necessary to parameterize and adjust the model more than once (e.g. in newly planted and developing orchards, orchards where some major modifications have been made, by using it for different apple cultivars, or for calculation of foliar pest effects). In most cases it is sufficient to parameterize wood surface area, numbers of long shoots and spurs, spacing of trees, numbers of flowers, and latitude. However, often the multiple specific input data or relationships needed are not available.

After a parameterization some current weather and phenology inputs are needed to run the model. These general inputs include daily minimum and maximum temperatures, total daily radiation, and date of bud break (to initiate the model). The weather inputs were kept as simple as possible to extend the range of situations that would have the required data.

2.2.2 Submodels

The original MaluSim model mainly consists of five submodels (Figure 1), with interactions between them.

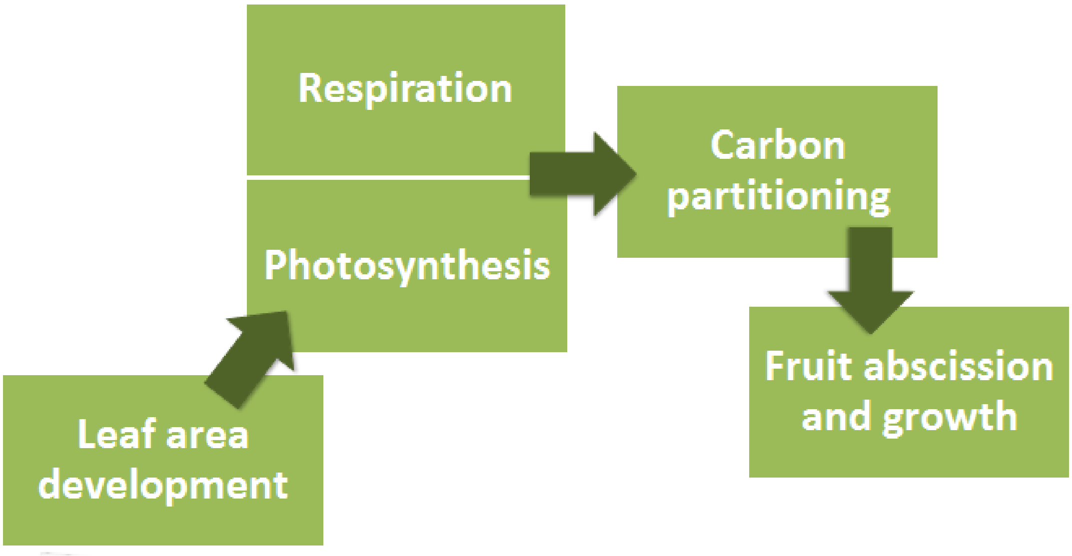

Figure 1: Schematic diagram of the main five original submodels of MaluSim, including a simplified representation of interactions between single submodels.

2.2.2.1 Leaf area development and leaf abscission submodel

For the calculation of photosynthesis and respiration of a tree, leaf area estimation is essential. Therefore, a specific submodel has been developed to calculate leaf area development and leaf abscission. JOHNSON & LAKSO (1985) found that leaf area development of apples is quite consistent as a function of temperature accumulation. Originally, they used a degree day approach with a 4 °C base (DegDay) to calculate the leaf area increment (LA_{incr}) per shoot (in m^2) per day (LAKSO & JOHNSON, 1990):

$$LA_{incr} = 0.00008 * DegDay \tag{I}$$

Average temperature in MaluSim is calculated by adding maximum and minimum daily temperature, and dividing the result by two, to get the average temperature. From the result a base temperature of 4 °C is subtracted. This base temperature is thought to be the minimum temperature necessary for growth (JOHNSON & LAKSO, 1985). The leaf area increment per shoot is then multiplied with the total number of growing shoots at that time. The fraction of growing shoots has been estimated as a function of accumulated degree days (LAKSO & JOHNSON, 1990). Daily values are accumulated over time. There exist cultivar differences for leaf area increment (JOHNSON & LAKSO, 1985).

The original leaf area development submodel has been improved by splitting the leaf area development calculation into one for long and one for short shoots (spurs) (LAKSO et al., 2001b). For each shoot type, leaf area development is calculated based on growing degree day accumulation, rate of leaf area expansion per degree day, total shoot number, and fraction of growing shoots at the particular time (LAKSO et al., 2001b). For the calculation the original method has been maintained. Short shoot leaf area increment was set at 0.00004 m^2 per DegDay per shoot, while the one for long shoots stayed at 0.00008 m^2 per DegDay per shoot (LAKSO et al., 2006a). Since the understanding of shoot termination is limited and is not clearly related to carbon, the calculation in MaluSim was artificially constrained to represent average conditions (LAKSO et al., 2001b). For a default, it is assumed that the final active shoots terminate at about 500 DegDays for spurs and 900 DegDays for long shoots. Leaf abscission is calculated similar to chill unit models as a function of cumulative daily minimum temperatures below 5 °C (LAKSO et al., 2001b).

2.2.2.2 Photosynthesis submodel

One major submodel for carbon balance calculation is the photosynthesis submodel, which gives the amount of assimilates (carbon). In MaluSim, the daily photosynthesis integral was calculated as a daily canopy light response according to CHARLES-EDWARDS (1982) from maximum photosynthetic rate, photochemical efficiency, daily integral of light, day length, canopy extinction coefficient and leaf area index (LAI) or fraction of available light intercepted (LAKSO & JOHNSON, 1990). Daily gross photosynthetic rate (P_{daily}) per unit ground area allotted per tree (in g CO_2 m^{-2} day^{-1}):

$$P_{daily} = \alpha * S * h * P_{max} * [1 - \exp(-k * LAI)] / (\alpha * k * S + h * P_{max}) \tag{II}$$

α : leaf photochemical efficiency or quantum yield in µg CO_2 $Joule^{-1}$ total radiation
S : daily integral of total radiation on a horizontal surface in MJ m^{-2} day^{-1}
h : day length in seconds
P_{max} : rate of light saturated leaf photosynthesis in g $m^{-2}s^{-1}$
k : canopy light extinction coefficient
LAI : leaf area index

Additionally, the temperature effect on photosynthesis is included as a fractional reduction multiplier of the leaf photosynthetic rate. The used relationship gives a maximum photosynthesis at about 28 °C, and zero at 0 °C and 44 °C (LAKSO & JOHNSON, 1990).

The original model of 1990 dealt with canopies as continuous structures (LAKSO & JOHNSON, 1990; LAKSO, 1992), which lead to significant errors in wider spaced single row orchards. To solve this problem the approach developed by JACKSON and PALMER (1979) was used. The light interception of discontinuous canopies is separated into two components: T_f, which is the part of daily total light transmitted to the floor between the trees, and T_c, which is the light that is transmitted to the ground by passing through the canopy (LAKSO, 1992). The maximum potential light interception by the canopy is termed F_{max}, and is equal to daily incident light input reduced by the fraction of light that never strikes the canopy ($1-T_f$). In a mature orchard a constant F_{max} can be used, because a mature orchard has little change in the potential solid canopy interception. In young or very vigorous orchards the change of maximum canopy dimensions can be significant during the season and F_{max} can be made a function of time (LAKSO, 1992).

In 2006 a major modification of the photosynthesis submodel was made because of some problems by simulating discontinuous orchard canopies. The original light interception term within the canopy photosynthesis equation has been corrected according to JACKSON & PALMER (1979; 1980) and PALMER (1989b), by using an asymptote in the normal Beer's Law light interception equation that relates interception to leaf area index, a canopy light extinction coefficient, and the estimated maximum light interception that would occur for an opaque tree (LAKSO et al., 2006a).

$$Light\ interception = 1 - e^{\left(-k * \left(\frac{LAI}{F_{max}}\right)\right)} \tag{III}$$

For the ‘standard’ spindle tree an F_{max} asymptote of 0.7 was used, and this value is supposed to be reasonable for many mature orchard systems today (LAKSO et al., 2006a). The extinction coefficient k varied usually from 0.4 to 0.6 depending on the relative ratio of spurs versus extension shoots. Spur canopies have leaf clumping due to the rosette growth habit and then k values as low as 0.3 can occur. k values of 0.4 to 0.45 are thought to be appropriate for mature spindle trees. Additionally, calculations to adjust the day length based on latitude have been inserted (LAKSO et al., 2006a).

In the version of MaluSim used in this thesis photosynthesis is at first calculated on a unit ground area basis, which is then in a second step converted to total photosynthesis per tree (by multiplication with ‘Areapertree’). Photosynthesis per unit ground area is calculated by using leaf photochemical efficiency (PChemEff), daily integral of total photosynthetically active radiation (PAR) incident on a horizontal surface (TotPAR), daylength, rate of light saturated leaf photosynthesis per unit leaf area dependent on temperature (PmaxTadj), canopy light extinction coefficient k (CanopyK), F_{max} (Fmax), and LAI (LAIndex):

$$\frac{\mathrm{PChemEff} * \mathrm{TotPAR} * \mathrm{DayLgth} * \mathrm{PmaxTadj} * \mathrm{Fmax} * (1 - \mathrm{EXP}(-\mathrm{CanopyK} * (\mathrm{LAIndex}/\mathrm{Fmax})))}{\mathrm{PChemEff} * \mathrm{CanopyK} * \mathrm{TotPAR} + \mathrm{DayLgth} * \mathrm{PmaxTadj}} \tag{IV}$$

There is a modification of the canopy photosynthesis model that allows direct input of measured light interception in place of the Beer’s Law submodel if such data is available. Additionally, a pest treatment effect on photosynthesis can be manually included.

2.2.2.3 Respiration submodel

The second important parameter for carbon balance calculation is respiration, which is calculated using the respiration submodel. Respiration is calculated as an exponential response of respiration rate (R) to temperature (LAKSO & JOHNSON, 1990):

$$R = a_r * \mathrm{e}^{k_r * T} \tag{V}$$

a_r : R at T = 0 °C

k_r : temperature coefficient of R

T : temperature in °C

Respiration is calculated for each type of organ and there exist specific coefficients for fruit, wood, and leaf respiration. Fruit respiration rates are based on fruit fresh weight, while leaf and wood respiration rates are based on their surface areas (BUTLER & LANDSBERG, 1981; LAKSO & JOHNSON, 1990). The coefficient k_r differs between plant organs but stays the same during the season for wood and leaf respiration. a_r always varies during the season and is specific for the tree organ. For fruits a_r and k_r vary seasonally. Total respiration per tree is the sum of fruit, wood, and leaf respiration (in g CO_2/day).

2.2.2.4 Carbon partitioning submodel

Available carbon for partitioning (daily carbon balance) is calculated from canopy photosynthesis minus organ respiration. The partitioning of the accumulated carbon has been adapted from the kiwifruit model of BUWALDA and co-workers (BUWALDA et al., 1990; BUWALDA, 1991). Demand is defined as the maximum dry matter growth rate of each organ, estimated from growth studies under assumed optimum conditions, and a temperature response is included. The quantity of the particular organ and the estimated maximum dry matter growth rate are used to calculate the total carbon demand for the particular organ type (LAKSO et al., 2001b).

Carbon is partitioned equal to the demands of organs when sufficient carbon is available to support all the demands. This allows all organs to grow at their maximum possible rate. When carbon supply is lower than total demand, carbon is partitioned based on a prioritization according to a relative sink strength (RSS) factor. The RSS factor has been estimated for each organ type and the sum of all RSS factors is one (LAKSO et al., 2001b). The priority order is: “shoots>>fruits>roots=wood”. The relative partitioning of carbon to a given organ is calculated by:

$$RP_i = Demand_I - (Demand_I\,(1 - RSS_i) * (1 - (Carbon_{avail} / Demand_{total}) \tag{VI}$$

RP_i : *relative partitioning to a given organ*

RSS_i : *relative sink strength of a given organ*

$Demand_I$: *calculated carbon demand of a given organ at a given stage and temperature*

$Carbon_{avail}$: *available carbon*

$Demand_{total}$: *total demand for carbon*

At the beginning of the season shoots are very active and receive most carbon, but later, when shoots terminate their growth demand, the carbon partitioning pattern changes and fruits and other organs receive more carbon, even though the RSS values remain the same throughout the season (LAKSO et al., 2001b). Overall, the carbon amount that is partitioned to each organ type depends on the individual demands, the number of actively-growing organs of the particular type, and whether carbon supply is sufficient or limited.

2.2.2.5 Fruit growth and abscission submodel

MaluSim calculates fruit growth and abscission based on available carbon supply to fruits. Fruit abscission is supposed to occur if fruit growth rate is not maintained above a critical rate of 60 % of the rate of the fastest-growing fruit (LAKSO et al., 2001b). This has been determined in field experiments, where 'Empire' fruits with a growth rate of 60 % or less were usually abscised by the tree. The critical growth rate is expressed relative to the fastest-growing fruits and not to any specific absolute growth rate, because this relationship was more consistent (LAKSO et al., 2001b). Absolute growth rates may be low due to lack of support for growth, leading to abscission, or to cold temperatures which generally do not lead to abscission.

The fruit growth and abscission submodel compares the amount of fruit growth supported by the carbon partitioned to fruit (3-day running average) to the maximum expected growth rate for that day (based on a maximum growth rate curve adjusted for temperature, and number of fruits). A 3-day running average of available carbon was used to simulate the known buffering of tree responses to short-term daily weather variations (for example, heavy shade for one single day has no effect on early fruit drop, but 2 days and 3 days have increasingly strong effects on drop). The above described relationship is used to calculate "physiological fruit abscission" and the number of current fruits is adjusted for the next day. Carbon supported fruit growth is accumulated and total crop weight and mean fruit weight is calculated (LAKSO et al., 2001b). MaluSim only calculates fruit abscission based on carbon balance, but it is possible to add empirical pollination and hand thinning factors to over-ride the basic parameter values.

To achieve best results it is necessary to use cultivar-specific fruit growth and demand curves as well as cultivar-specific abscission curves (LAKSO et al., 2006a). The fruit growth and abscission submodel has only been published in parts and for most simulation runs fruit number has been set to a fixed specific number (LAKSO, 2011; LAKSO & ROBINSON, 2015). It has not yet been confirmed to calculate realistic final fruit numbers. Therefore the fruit growth and abscission submodel has to be tested und further developed. Further information about the submodel can be found in chapter 2.3.4.

2.3 Fruit development, thinning and the fruit growth & abscission submodel

As described in the introduction, one of the most important management decisions for apple growers is the one concerning thinning. The farmer has to thoroughly think about when to thin, which chemical or method to use, it can be different for a particular cultivar, and is well known to be very variable from year to year even with the same thinning treatment. The MaluSim model is thought to be able to help making these decisions, and simple comparisons of total carbon supply to total demand, have been useful for growers in the US. However, since the fruit growth and abscission submodel has not been working properly and not been used for practical applications, at first, it has to be modified or further developed.

2.3.1 Apple fruit development

In apple, flower bud development can be divided into several stages including flower induction, initiation, and differentiation. It extends over two consecutive seasons (HÄTTASCH et al., 2008), and thus starts one season before blooming and fruit development. Flower bud induction is the transition of the meristem from vegetative to reproductive growth, and is assumed to happen about 3 to 6 weeks after bloom (BUBÁN & FAUST, 1982; FOSTER et al., 2003) for next year's flowers, although tip-bearing varieties can set flowers later. Although the carbohydrate requirement for flower induction is extremely small, it happens at the same time as intense cell division in the fruits takes place (YURI et al., 2011) and appears to be a weak sink. A heavy crop load can delay, decrease or even inhibit flower induction, with the result of fewer flowers in the following year (BUBÁN & FAUST, 1982; PALMER, 1992) and therefore the risk of inducing alternate bearing.

Apple flower clusters usually contain about five to seven flowers. For adequate yields, a sufficient proportion of flowers have to be pollinated and fertilized (WERTHEIM & SCHMIDT, 2005). Many apple cultivars show self-incompatibility and therefore cross pollination is needed. Honeybees (*Apis mellifera*) are the numerically most important apple pollinators (RAMÍREZ & DAVENPORT, 2013). Date of full bloom is primarily driven by spring temperatures and differs between cultivars, between years for one cultivar, and between growing regions.

Apple fruit development consists of a phase, where mainly cell division occurs, followed by phase with mainly cell expansion. At three to four weeks after full bloom cell expansion predominates, but cell division still takes place (GOFFINET et al., 1995). Cell number attained at the end of the cell division phase sets the potential for final fruit size in apples

(SMITH, 1950; GOFFINET et al., 1995). Temperature during cell division phase has a large effect on final fruit size (LAKSO et al., 1995; WARRINGTON et al., 1999; STANLEY et al., 2000). Besides temperature, endogenous hormones, nutrients, water relations, and plant carbon balance are supposed to play a major role in cell division (CORELLI-GRAPPADELLI & LAKSO, 2004). But the current understanding on how cell division and expansion are regulated in apple is still limited. Diameter increase of apples can be represented in terms of a sigmoid pattern. When weight or volume is considered as a measure of fruit growth the growth pattern is expolinear: exponential growth during cell division phase, followed by the cell expansion phase with linear growth (LAKSO et al., 1995; STANLEY et al., 2000).

2.3.2 Natural fruit drop

During fruit development of apple there are several phases of flower or fruitlet drop. Shortly after bloom there is the first main drop of unfertilized flowers (HANDSCHACK, 1997). A second, very small drop often occurs at about three to four weeks after petal-fall, when the endosperm in the seed becomes cellular (BERÜTER & DROZ, 1991). The third phase of dropping is called the ‘June drop’ (northern hemisphere) in Europe and is the most important one for growers. A last natural fruit drop may occur shortly before harvest due to a premature formation of the abscission layer (TROMP & WERTHEIM, 2005).

During the ‘June drop’ phase there are waves of drop that vary from year to year. Fruitlets of varying sizes are shed and drop can range from heavy to nearly zero. There are not only large variations in the severity of the final drop between cultivars, but also between seasons and sites. The mechanism is not well understood but large fruitlets with a high number of developing seeds have a higher chance to persist on the tree than smaller fruitlets with low seed numbers (HANDSCHACK, 1997; TROMP & WERTHEIM, 2005). But numerous hormonal and assimilate based tree factors, like vegetative growth, flower quality, tree age, cultivar and rootstock, but also environmental factors like temperature, water supply and light conditions have an influence on the severity of fruit abscission (BYERS et al., 1990a; DENNIS, 2000; BANGERTH, 2004). Fruit abscission is supposed to be a self-regulating mechanism of the tree to adjust the number of fruits to a level, which can be supported under the prevailing environmental conditions (BANGERTH, 2000). But for commercial apple production this self-regulatory mechanism of the grown cultivars is insufficient to reduce fruit load to an adequate final crop load and fruit size (IWANAMI et al., 2012).

At the beginning of a season the energy resources needed for growth and flowering are derived from reserves. This gradually shifts around flowering time and the main part of energy needed for fruit development during the season is produced via photosynthesis (CORELLI-GRAPPADELLI & LAKSO, 2004). Primary spur leaves are the earliest carbon contributors to fruit growth (CORELLI-GRAPPADELLI & LAKSO, 2004) and a well exposed spur canopy is essential for early fruit carbon supply and thus total tree yield (WÜNSCHE et al., 1996; WÜNSCHE & LAKSO, 2000). Long shoot export of carbon starts later (CORELLI-GRAPPADELLI et al., 1994) and within the first 4-5 weeks after full bloom there is a period where carbon supply may be limiting (CORELLI-GRAPPADELLI & LAKSO, 2004). Overall, spurs support fruit growth earlier than long shoots and are very important for successful apple production. After the canopy reaches its full photosynthetic potential and crop levels are adjusted by thinning, carbon supply usually exceeds the total fruit demand until shortly before harvest, where shortages may occur again (CORELLI-GRAPPADELLI & LAKSO, 2004).

2.3.3 Thinning

Fruit thinning has been practiced for many years and is an essential part of commercial apple production, but it remains an unpredictable part with large variations from year to year and within years (WERTHEIM, 2000; DENNIS, 2003; ROBINSON & LAKSO, 2011). It is one of the most important management decisions to achieve the optimal crop of high quality apples (LINK, 2000) and the commercial success of growers. Insufficient thinning means higher costs for later hand thinning in the current season and lower flower numbers in the next season, with the risk of biennial bearing. Over thinning means a loss of possible saleable apples itself, no optional hand thinning of damaged fruits, low quality (bitter pit, flesh browning, short storage life) and unwanted big-sized apples. Because thinning of large numbers of trees by hand is neither practical nor economical (WERTHEIM, 2000), various thinning methods have been developed. But thinning methods and regulations (release and withdrawal of chemicals from the market) vary from one country to the other and also from one year to the next in any particular country.

The possible thinning period is quite long, but there are regulations as well as some phases that are not very popular among growers. Thinning is possible at bloom, petal fall, and during fruit development. Most farmers do not like early thinning of flowers, since they do not want to eliminate a portion of flowers before adequate fruit set is ensured. But early thinning is required for cultivars with a high likeliness of alternate bearing and when climatic conditions are favorable for fruit set (WERTHEIM & WEBSTER, 2005). Early thinning (at bloom) resulted in much higher return bloom than thinning at any later stage (BYERS & CARBAUGH, 2002). Late thinning (after 21 DAFB) resulted in inadequate return bloom in the following year.

Often used chemical methods of flower thinning are spraying with caustic compounds (e.g. ammonium thiosulphate (ATS) (WERTHEIM, 2000), or lime sulfur (GUAK et al., 2004)), or with chemicals that enhance ethylene formation (e.g. ethephon (EBERT & BANGERTH, 1982)), which then causes fruit drop. For post-bloom fruit thinning, also growth regulators such as auxins (e.g. naphthalene acetic acid (NAA), amide of naphthalene acetic acid (NAAm)) or cytokinins (e.g. 6-benzyladenine (BA)) (YUAN & GREENE, 2000; SCHRÖDER et al., 2013), as well as metamitron, a photosynthetic inhibitor (BASAK, 2011), can be used. Non chemical methods of thinning are artificial shading (BYERS et al., 1990b; ZIBORDI et al., 2009; BASAK, 2011), mechanical (SOLOMAKHIN & BLANKE, 2010) (e.g. Darwin 300, string thinner (SCHUPP et al., 2008)), and hand thinning.

Factors that increase or decrease natural fruit drop are known to also influence the effectiveness of chemical thinning. In addition, chemical thinning efficiency is also greatly influenced by the efficiency of spraying (volume, coverage), spray additives (surfactants), timing of thinning, compatibility with other chemicals applied at the same time (WERTHEIM & WEBSTER, 2005). Additionally, large differences in sensitivity of different apple cultivars to thinning agents have been found (COSTES et al., 2006). The many field experiments of the past were able to identify factors that appear to relate to thinning response, but the underlying mechanisms are not fully understood and described.

High temperatures enhance the effect of thinners, for cool weather the reverse is true (WERTHEIM & WEBSTER, 2005). Higher night temperatures, especially on the day of the application plus the next day, were found to be more highly related to chemical thinning than daytime temperatures or daily average temperatures (BYERS, 2002). Beside temperature, light conditions play an important role for thinning efficiency. While cloudy, low light conditions before or after thinner application increase the effect of many thinning agents, sunny conditions often lower the thinning effect (WERTHEIM & WEBSTER, 2005). As already mentioned, artificial shading also can be used by itself as a thinning method, which additionally underlines the significance of prevailing light conditions for thinning responses. This sensitivity changes during the season. Complete shading of whole trees for 5 days during early fruit development has been found to cause a total fruit drop, while applied after June drop no fruit abscission occurred (BERÜTER & DROZ, 1991). These findings indicate that weather effects on tree carbon balance are one of the major players in apple thinning and that this is one of the main reasons for year-to-year variability of thinning responses and natural fruit drop. Therefore, large uncertainties for the growers remain, which might be removed or at least reduced through the use of carbon balance modeling. Carbon balance modeling has already helped to explain some of the great variations in fruit drop (LAKSO et al., 2006b; PARRA-QUEZADA et al., 2006).

2.3.4 MaluSim fruit growth and abscission submodel

The fruit growth and abscission submodel of MaluSim is mainly based on general relationships extracted from the developers own experimental data and from other published data. In general, the time of greatest carbon supply-to-demand deficit occurs at about one to three weeks after bloom, when both shoots and fruits need high amounts of assimilates for their growth (LAKSO, 2011). During this time, shoots have a higher priority than fruits. It has been shown that extension shoots use the produced carbon of their leaves for their own growth until they have developed a critical level of leaf area of about 10 - 12 leaves per shoot (CORELLI-GRAPPADELLI et al., 1994). When carbon supply was limited by low light, fruit dry matter growth was reduced much more than shoot growth (BEPETE & LAKSO, 1998). The primary carbon source for fruit growth during the early period of growth are the spur leaves (LAKSO, 2011).

It has been found for apple, that fruit growth during the early period strongly affects set or abscission. Fruits that markedly slowed down their growth rates for a few days were destined to abscise (LAKSO et al., 2001a). This finding is a basis of the fruit growth and abscission submodel of MaluSim (LAKSO et al., 2006a; LAKSO, 2011). The simplification used in the model calculates the actual amount of carbon which supports fruit growth. This supported fruit growth is then compared to a pre-determined seasonal demand, in this case to a maximum growth rate for a specific cultivar. According to the percent-of-maximum growth rate, the model determines how many fruit will be abscised (LAKSO et al., 2006a) and re-sets the fruit number for the next day (LAKSO, 2011).

The maximum possible fruit growth rate has been estimated from experiments. For the estimation, curves of weight over time of fruit on very lightly-cropping trees, where no fruit carbon deficit is assumed, were used. Maximum possible fruit growth rate is temperature dependent, which is also included in the model. Daily dry weight increase is supposed to equal the amount of carbon available for fruit growth and is related back to fresh weight to calculate fresh weight growth (LAKSO, 2011). The calculated fresh weight growth is then divided by the number of current fruit to estimate mean fruit weight. For best results it is necessary to use cultivar-specific fruit growth and abscission curves and LAKSO et al. (2001b) monitored abscission patterns for the cultivars ‘Empire’, ‘Gala’ and ‘Delicious’.

Important for the fruit growth and abscission submodel (Figure 2) is the carbon that is available for fruits (CO2toFrts). This CO2toFrts is an output of the carbon partitioning submodel (see chapter 2.2.2.4).

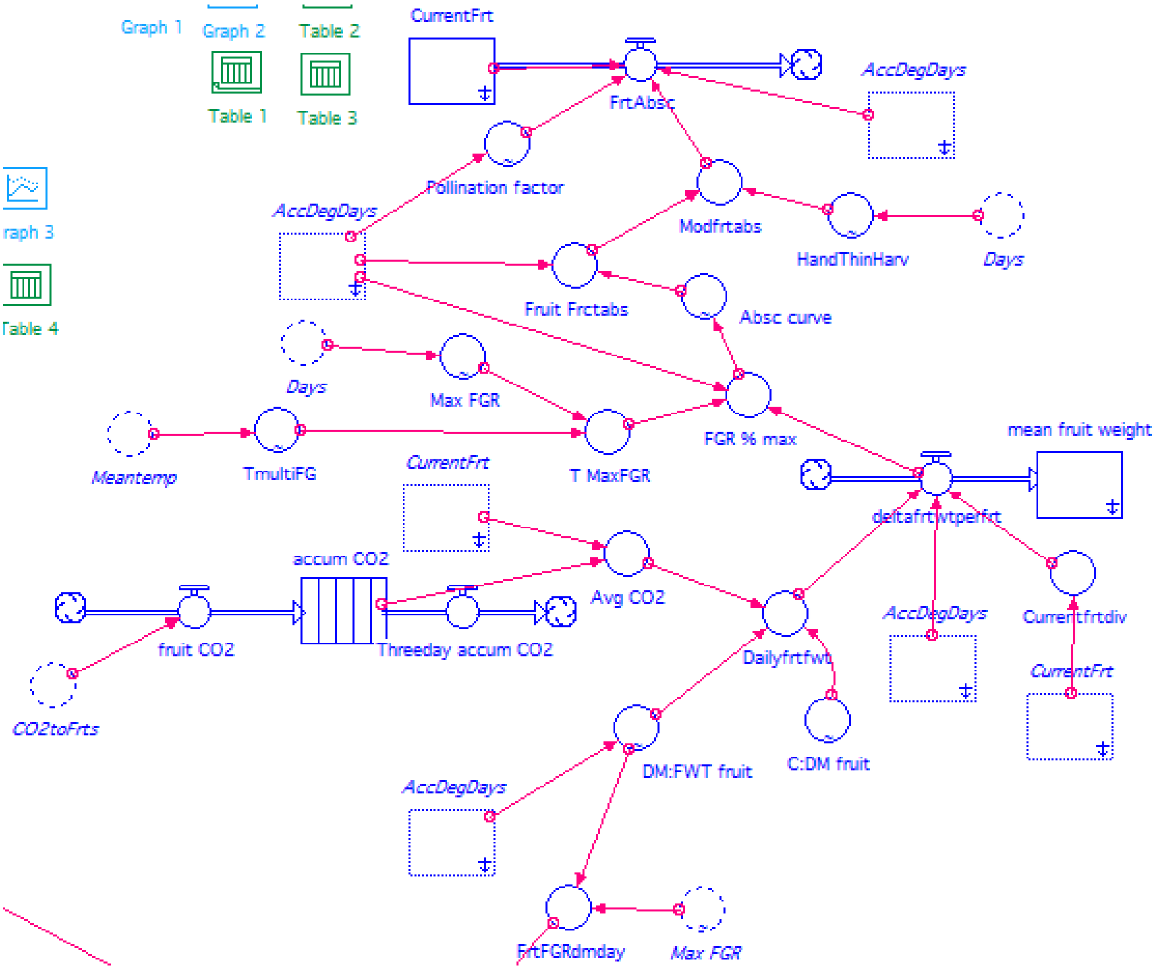

Figure 2: Image of the graphical interface of the MaluSim fruit growth and abscission submodel in STELLA®.

To buffer short time effects the CO2toFrts is accumulated and a running 3-day average is calculated. Due to this the fruit abscission is responding only to longer variations in weather conditions. This is based on the observation that trees also have a buffer and do not respond to very short time effects. The calculated average CO2 which is partitioned to the fruits (Avg CO2) is then transformed into the daily carbon partitioned to fruit in terms of fruit fresh weight (grams) (Dailyfrtfw). This is conducted by using a carbon dioxide to dry matter converter (C:DM fruit), followed by a dry matter to fresh weight (DM:FWT fruit) converter. The Dailyfrtfw divided by the number of fruits (CurrentFrt) determines the daily available fresh weight (grams) available to each fruit (deltafrtwtperfrt). The fruit development submodel begins after 170 accumulated degree days, base 4°C after bud break. Before 170 accumulated degree days, flowers are estimated to grow slowly and not require significant amounts of carbon. An accumulation of the deltafrtwtperfrt gives the mean fruit weight in grams.

As already stated, the maximum possible fruit growth rate and the fruit growth rate supported by carbon are compared and then the amount of fruit abscission is determined. This maximum fruit growth rate (Max FGR) has been determined empirically. It depends on temperature and therefore has a temperature multiplier (TmultiFG). The temperature adjusted maximum growth rate and the deltafrtwtperfrt are compared and the percentage fruit growth rate of the maximum temperature adjusted fruit growth rate (FGR % max) is obtained. The FGR % max is converted into the fruit abscission curve (Absc curve), which is based on 'Empire' fruit thinning and shade studies conducted over multiple years. The abscission curve is used until 720 accumulated growing degree days, which on average corresponds to 39 days after full bloom. After this period it is assumed that the tree retains the current fruit number.

It is possible to add a hand thinning effect (HandThinHarv) that allows a specified reduction in fruit numbers at any particular day, either early or to simulate harvest. In general, the pollination factor assumes that one third of the fruit will be successfully pollinated, but the factor can also be changed manually to better fit to field conditions. Before 190 accumulated growing degree days (point of full bloom) only the pollination factor is used for the calculation of abscission. After this point, fruit abscission rate is calculated by multiplying current fruit number by abscission factor or hand thinning factor depending on which is the active process. The calculated fruit abscission rate is used to change the current fruit number for the next day.

2.3.5 Current method on how to use MaluSim for thinning advice in the USA

Although the fruit growth and abscission submodel has been developed based on the previously presented relationships, it showed oversensitive behavior. For this reason, LAKSO & ROBINSON (2015) used the model to help understand variations in fruit drop around thinning time by using a 'standard tree' with fixed fruit numbers instead of using the fruit growth and abscission submodel (LAKSO et al., 2006b; LAKSO, 2011). This means for example to use 'Empire/M.9' slender spindle at 2000 trees/ha with a fixed fruit number of 300 fruit/tree, which equals a level which is at the high end of what is possible to carry for that kind of tree in a good year. Commercial crop level typically is 200 to 250 fruits (LAKSO & ROBINSON, 2015). To determine if carbon balance would provide useful explanations of thinning variations, weather data from different years were entered into the model and the calculated carbon balance (total C supply to total C demand) examined for periods of especially positive or negative carbon balance. These were found to coincide quite well with experimental thinning trial results where the same thinners were applied each year at about 4 day intervals after bloom (ROBINSON & LAKSO, 2011). Additionally, ROBINSON & LAKSO (2011) found out that balanced years with no particularly good or poor supply led to a traditional pattern of chemical thinning response with the greatest fruit drop peaking at about 10 to 12 mm fruit size (ROBINSON & LAKSO, 2011). At greater fruit sizes (18 to 20 mm) the effectiveness of thinning is reduced again. This general pattern is related to carbon deficits, which appear to give rise to the year to year variability (ROBINSON & LAKSO, 2011). It was also found that the strongest effect of poor carbon balance appeared to occur in the first 3-4 days after treatment. MaluSim helps growers in the USA by providing an estimate of the achieved thinning within four to seven days after thinner application, which would allow an informed decision of whether additional sprays are needed or not. With an accurate weather forecast, MaluSim is able to provide predictions of thinning efficacy even before sprays are applied (ROBINSON & LAKSO, 2004, 2011). But it only addresses carbon-related aspects and thus does not explain variations due to other factors (LAKSO & ROBINSON, 2015). It has been used in several regions in the US to predict thinning response with good but not perfect success (LAKSO & ROBINSON, 2015).

There also exists an online version of the model for the USA (NEWA CORNELL UNIVERSITY, 2015) and also some blogs of scientist using the model and giving general advices for particular regions (VIRGINIA STATE UNIVERSITY, 2014; PENN STATE UNIVERSITY, 2015). The online model allows the grower to select their choice of weather stations and enters the budbreak date. The system gathers the requested data, runs the simulation with the default tree parameters, and provides the data and model outputs as well as recommendations for adjusting thinner concentrations. Many apple growers in the eastern and midwestern US used the model and reported very useful results (LAKSO, 2019). The model is used as a general guide and according to LAKSO & ROBINSON (2014) the US growers have found the model to be a useful input to their thinning decisions. This method has been widely used because the fruit growth and abscission submodel was not completed and validated (LAKSO & ROBINSON, 2015). It is used to provide advices for the particular prevailing conditions, but not to correctly calculate final fruit numbers. Using a fixed number of fruits may also lead to a wrong calculation of carbon balance. Therefore, being able to use properly calculated fruit numbers might further improve the calculations of MaluSim, and hence the advices for the growers.

2.4 General physiology and water relations of apples

Beside thinning issues, another main concern of today's apple growers is whether additional irrigation will be necessary for future apple production because of the Changing Climate, or will only be an additional expense which will not pay out in the end. This issue applies for new apple orchards and does not only concern the possible advantage of being able to produce high quality apples in dry and hot years when orchards are mature. It also addresses the question of how beneficial is a faster establishment of newly planted apple orchards and will this lead to an earlier payout of planting costs? For this reason and to be able to model water effects it is very important to fully understand water relations of apple trees and know its effects on whole apple tree physiology.

2.4.1 Light interception

Dry matter production in apples is known to be highly related to intercepted light (PALMER, 1989a; LAKSO, 1994). Light interception (LI) and distribution within tree canopies depend on diverse inter-related factors (WILLAUME et al., 2004). Maximum potential yield is usually directly proportional to intercepted light (JACKSON, 2003). However, for commercial apple production, high LI of apple trees does not automatically translate into an increased yield of marketable fruit (LAKSO, 1994; WÜNSCHE et al., 1996; WÜNSCHE & LAKSO, 2000). Understanding the basic light relationships of trees is essential for their effective manipulation and to maximize its production efficiency.

LI of apple trees depends on number and length of long shoots and of spurs, and their associated total leaf area, as well as on leaf transmission and reflection, leaf angle, folding and total distribution, but also on the height of trees, tree architecture, and the particular training and planting system (JACKSON, 1980). During tree establishment the number of long shoots and spurs, and height of trees increases, and LI increases until reaching a maximum on mature trees. The individual size and area of leaves is affected by genetics in terms of scion and rootstock (WILLAUME et al., 2004). There exist thousands of scion cultivars, and apple cultivars which were classified according to their architecture into four different growing types: columnar, spur, spindle, and tip bearer (LESPINASSE, 1992), but especially the rootstock has a major effect on tree size and thus on LI of apple trees. Nowadays, for thin slender spindle trees in commercial apple production in Germany mostly M.9 type rootstocks are used. For any combination commonly used training systems in commercial apple production, for example slender spindle, V-trellis, Y-trellis, and central leader, will affect the LI. Especially within-tree shading has negative effects on fruit quality and is decreased through modern training procedures (WILLAUME et al., 2004).

Overall, leaf area is the most important parameter for tree LI. A possible way to estimate tree leaf area is to use trunk cross-sectional area (JACKSON, 1980). However, for mature commercial trees, which are pruned regularly to maintain the tree in an allotted space, this method is not very reliable anymore. Trunk girth and cross-sectional area continue increasing while leaf area is contained through pruning (JACKSON, 2003). Widely spread expressions related to LI are LAI, k and F_{max}. LAI is leaf area index, which is the m^2 leaf area per m^2 ground area allotted per tree. Light extinction coefficient k depends on average spectral properties of the leaves and their orientation in relation to the spatial distribution of radiation (JACKSON, 2003). In apple, k usually ranges from about 0.44 for spurs to 0.77 for extension shoots (JACKSON, 1980). F_{max} is the maximum fractional LI which would occur if trees were opaque (JACKSON, 2003) since in orchards some light in the alleyways never passes through the trees. In general, north-south hedgerows are preferable to east-west ones due to LI and light distribution. There exist various models and methods to assess LI of trees (e.g. the ones by JACKSON & PALMER (1980; 1986, 1989b), CHARLES-EDWARDS (1982), WÜNSCHE et al. (1995), GREEN et al. (2003), OYARZUN et al. (2007), SINOQUET et al. (2008) or by DA SILVA et al. (2014)). PEREIRA et al. (2007) found a relationship between daily canopy transpiration and daily net radiation multiplied by LAI for apple. AUZMENDI et al. (2011) confirmed the relationship and showed a potential application of intercepted PAR (combined with VPD) to estimate the amount of needed irrigation water. Not only total tree LI is important, but whether light is intercepted by spurs or by extension shoots (WÜNSCHE & LAKSO, 2000), as stated earlier.

Physiological traits influenced by light environment are for example bud differentiation, leaf type, and thus photosynthetic potential of leaves, and ratio of spur to long shoot leaf area (PALMER, 1989a). The partitioning of resources is also largely controlled by light (CORELLI-GRAPPADELLI, 2003). Interestingly, no effect, neither positive nor negative, of shading for several days 3 weeks after bloom has been detected for shoot length growth rates per day while fruit growth was strongly inhibited (BEPETE & LAKSO, 1998). But JACKSON & PALMER (1977) found a reduction in number and weight of new shoots, and in fresh weight per unit length of shoot, for apple tree heavily shaded over long periods. Photosynthesis (see Chapter 2.4.2) is one of the most important processes in plants and highly dependent on light. But LI also directly affects fruit quality. Shading of fruits is known to affect fruit size, color, soluble solids concentration, mineral elements content (e.g. calcium) and firmness (JACKSON & PALMER, 1977), while too much light can lead to ‘sunburn’ of fruits (SCHRADER et al., 2003).

Overall, LI of apple trees is important in many aspects. A high and favorable LI leads to high quality apples. LI is one of the main drivers for assimilate production and can be optimized for mature trees by an appropriate training system. Much is known about long shoot and spur LI in apples. A fast vegetative growth during the establishment phase is highly wanted and leads to an increased LI and to an early achievement of final tree size.

2.4.2 Photosynthesis

Photosynthesis is the first step in a complex series of biochemical processes. Most products of photosynthesis are translocated and further metabolized, degraded in respiration, or stored as reserves (TROMP, 2005). Apple trees are known to use the C_3 photosynthetic pathway to fix CO_2 and the major photosynthate in mature leaves is sorbitol (LOESCHER et al., 1982), followed by sucrose, starch, glucose and fructose (ZHOU et al., 2001; ZHOU & QUEBEDEAUX, 2003). Sorbitol is also the major translocated form of carbon in apples (LOESCHER et al., 1982).

In apple trees 'sun' and 'shade' leaves exist, depending on the light environment during leaf emergence and development (BÖHNING, 1948; BARDEN, 1978; FLORE & LAKSO, 1990). Sun leaves are capable of greater maximum photosynthesis, while shade leaves are generally more efficient at low light levels (CAMPBELL et al., 1992; CORELLI-GRAPPADELLI, 2003). Sun leaves have a greater specific leaf weight (MARINI & BARDEN, 1981) and a lower light transmittance, while reflectance of the two leaf types is similar (PALMER, 1977). Shade leaves typically have a reduced dark respiration rate compared to sun leaves (CAMPBELL et al., 1992). Reduced photosynthetic ability of shaded leaves does not appear to be readily reversible by re-exposure of the leaves through summer pruning (FLORE & LAKSO, 1990). Photosynthetic saturation in exposed apple leaves was found to be at about 1000 to 1200 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD) (PRETORIUS, 2006). FLORE & LAKSO (1990) surveyed 51 published articles and calculated a mean maximum photosynthetic rate of $15.7 \pm 5.6\ \mu mol\ m^{-2}\ s^{-1}$ for apple leaves. The optimum leaf temperature for photosynthesis was found to be 25 to 30 °C and high temperature effects were more profound under drought conditions (PRETORIUS & WAND, 2003). Maximum photosynthetic rate of apple leaves has been found to occur a few days before full expansion of the leaves (KENNEDY & JOHNSON, 1981; FUJII & KENNEDY, 1985), but mature apple leaves have minimal reductions for many months. Besides differences between leaves grown in full sunlight or in shade, no difference has been found between long shoot and spur leaves concerning their photosynthetic potential (BARDEN, 1978). Additionally, no significant difference in photosynthetic rate of different apple cultivars has been found. Environment, stage of development, and fruit load seem to have the greatest influence on photosynthetic rate of apple leaves (FLORE & LAKSO, 1990). Photosynthesis is highly affected by atmospheric CO_2 concentration (PAN et al., 1998; CHEN et al., 2002) and high diurnal CO_2 fluctuations have been measured in apple orchards (HAMACHER et al., 1994). Besides the described essential light quantity and CO_2 concentration, additionally temperature, relative humidity, crop load, nutritional factors, and water status can have major effects on photosynthesis of apple trees. WÜNSCHE et al. (2000) found a linear relationship between leaf photosynthesis and stomatal conductance, with stomatal conductance accounting for 80 % of the variance of leaf photosynthesis.

Environmental factors influence photosynthetic rate through stomatal and non-stomatal responses. Behavior of apple leaf stomates appears to be primarily regulated by light conditions (JONES, 1985; LAKSO, 1994). Stomatal conductance (g_s) is additionally affected by leaf temperature, vapor pressure deficit (VPD), mineral nutrition, and by soil and plant water status in the short term. Over the longer-term source-sink balance of the tree and more precisely current sink strength of plant organs has also been found to have an effect on the plants photosynthetic demand for CO_2 and on stomatal conductance (PRETORIUS & WAND, 2003). In general, apple leaves maintain a high leaf water use efficiency (WUE - defined as photosynthesis per unit of transpiration) throughout the season, depending on carbohydrate demand of the tree (PRETORIUS & WAND, 2003). Rapid or prolonged soil moisture deficit and VPD at fairly high levels (> 2.5 kPa) lead to stomatal closure in mature apple leaves.

The maintenance of leaf turgor under drought can be achieved by osmotic adjustment in plants. This is the accumulation of proline, sucrose, soluble carbohydrates, glycinebetaine, and other solutes in the cytoplasm to improve water uptake from the drying soil (ANJUM et al., 2011). Mature apple leaves were found to be capable of osmotic adjustment (DAVIES & LAKSO, 1979; FANJUL & ROSHER, 1984; LAKSO et al., 1984; WANG & STUTTE, 1992; WANG et al., 1995), while no evidence for osmotic adjustment was found for leaves at the growing shoot tip (LAKSO et al., 1984).

Intercellular CO_2 concentration (C_i) is an indirect indicator of stomatal limitation to photosynthesis. It is calculated from CO_2 and water vapor fluxes and allows to determine whether a reduction in net photosynthetic rate occurs due to stomatal closure (c_i decreasing), or is caused by non-stomatal limitations such as reduced light use efficiency (c_i increasing) (PRETORIUS & WAND, 2003). Stomatal closure reduces CO_2 supply, while nonstomatal limitation usually means damage to the photosynthetic apparatus (ZHANG et al., 2010). Besides stomatal conductance and biochemical capacity, mesophyll conductance has been found to be a third player in the process of photosynthesis (FLEXAS et al., 2012), but little is known about mesophyll conductance in apple trees.

Apple trees show a diurnal pattern of net photosynthetic rate, with maximum values occurring in the morning and then tend to decline gradually during the afternoon until sunset under normal field conditions (LANDSBERG et al., 1975; LAKSO, 1986; CHENG & LUO, 1997; WÜNSCHE et al., 2000; ZHOU et al., 2001). For apple trees growing in Girona (Spain), daily maximum stomatal conductance occurred early in the morning (between 8:00 and 10:00 a.m.) and decreased near midday (DOLTRA et al., 2007). A decrease in the afternoon has been associated with stomatal closure (VPD and temperature effects) or with build-up of photoassimilates (FLORE & LAKSO, 1990) which has been associated with crop load, but the understanding of mechanisms responsible for the diurnal pattern is still incomplete. Knowledge about seasonal patterns is sparse. CHENG and LUO (1997) found daily maximum photosynthetic rate to be high in spring, depressed in midsummer, recovering in late summer, and then declining again with senescence of leaves. In contrast, stomatal conductance has been low in spring, peaked during midsummer, remained relatively high in late summer and then declined.

The presence of fruit (high crop load) has been found to result in high photosynthetic rates (MONSELISE & LENZ, 1980; FUJII & KENNEDY, 1985; WÜNSCHE et al., 2000). PALMER et al. (1997) demonstrated a feedback effect of sink activity on the activity of source leaves. Leaf photosynthesis of non- and lightly cropping trees was reduced (PALMER et al., 1997). In addition, KLAGES et al. (2001) also found significantly reduced leaf photosynthetic rates on trees with low and no crop load during midday and late afternoon. However, they detected no crop load effect in the morning. This might be explained by accumulation of photosynthetic products in the leaf, resulting in feedback inhibition (KLAGES et al., 2001).

Apple leaves show a typical asymptotic photosynthetic light response curve (LRC) (FLORE & LAKSO, 1990). This leaf LRC differs for sun and shade leaves. In addition, the shape of LRCs of single leaves differs from LRCs of whole trees. A single leaf LRC reaches its maximum at lower PPFD levels than a LRC of whole trees. This also means that the compensation point occurs at a higher PPFD for the whole canopy compared to a single leaf (CORELLI-GRAPPADELLI, 2003). Whole tree photosynthesis equals the integrated sum of photosynthesis by leaves throughout the canopy volume. Thus, whole tree LRC is expected to vary as a function of sunlit in relation to shaded leaf area and the relative amount of irradiation available to the shaded leaves (LAKSO & MUSSELMAN, 1976; FLORE & LAKSO, 1990). It is a function of the amount of intercepted light, but it is influenced by the same factors like single leaf photosynthesis (BALDOCCHI & AMTHOR, 2001) and is highly affected by CO_2 concentration.

Drought negatively affects photosynthesis of apples (LAKSO, 1979; LANDSBERG & JONES, 1981; FLORE et al., 1985; JONES et al., 1985; FLORE & LAKSO, 1990; LAKSO, 2003; JIE et al., 2010). Water stress effects can be caused by soil moisture or by atmospheric water deficits or by both. VPD is important in fruit trees due to the very low hydraulic conductivity of the root systems (JONES et al., 1985). The magnitude and the diurnal course of photosynthetic rate of single leaves and whole trees are affected by water deficits. Apple trees show a single peaked CO_2 exchange during one day under cool and humid air and adequate soil moisture. When plants suffer from soil water deficits, the maximum photosynthetic rate shifts to an earlier point of the day (BALDOCCHI & AMTHOR, 2001). Indications have been found that with gentle to moderate water stress mainly stomatal limitations to photosynthesis occur, while under more severe water stress conditions nonstomatal limitations occur (FLEXAS et al., 2004; ZHANG et al., 2010). In addition, leaf growth and canopy development are negatively affected by water deficits (FERNANDEZ et al., 1997a). This can lead to a reduction of maximum possible tree photosynthesis caused by a reduced interception of light by drought stressed trees. There exist various models for tree canopy photosynthesis, with Farquhar's photosynthesis model (FARQUHAR et al., 1980) being a widely used one for C_3 plants. Photosynthesis is one of the main drivers of apple tree assimilate production and also of MaluSim carbon supply calculation. No evidence has been found that photosynthetic rate of apple trees changes during tree age. Although it is widely known that water stress leads to a reduced photosynthetic rate, so far, no scientifically sound relationship between photosynthetic rate and tree water status in apple has been described.

2.4.3 Respiration

Respiration is the process that provides the driving force for biosynthesis, cellular maintenance and active transport in plants (ATKIN & TJOELKER, 2003). This process oxidizes carbohydrates stepwise to water and CO_2, and supplies the plant with the energy needed for all cell activities (TROMP, 2005). Respiration takes place in all plant organs and carbon losses due to respiration affect net production of plant biomass (LE ROUX et al., 2001). Respiration rates change between for example day and night or between summer and winter. Respiration rate of apple trees is much lower at night than during the day, and lower in winter than in summer (WIBBE et al., 1994). Like most biological processes, respiration is highly affected by temperature (TROMP, 2005). The Q_{10} of respiration is often assumed to be 2 (i.e. respiration doubles per 10 °C rise in temperature) (ATKIN & TJOELKER, 2003). BUTLER and LANDSBERG (1981), however, reported a Q_{10} of 2.32 for apple tree respiration.

BEPETE & LAKSO (1997) constructed an initial seasonal fruit respiration model to estimate the effects of fruit development, daily temperatures, and fruit exposures on apple fruit respiration. Fruit respiration rates were found to be high during cell division phase and fruit specific respiration was correlated to relative growth rate (BEPETE & LAKSO, 1997). The cell expansion phase is thought to be energetically less costly than the cell division phase (LAKSO & DENNING, 1996).

2.4.4 Water relations of apple trees

Water is the greatest component of a tree by mass and almost all critical processes can be limited by water deficiency (JONES et al., 1985; LAKSO, 2003). Water consumption of apple orchards varies with tree characteristics, climate, and changes during the season. Transpiration is one of the main processes that affect water use of apple trees (NAOR, 2006). Leaves are the most active transpiring surfaces and intercept the radiation that drives transpiration (LAKSO, 2003), which makes tree water use highly dependent on leaf area and radiation interception. Total evapotranspiration of apple orchards can be divided into tree transpiration, evaporation from the soil, and transpiration from grass between rows (BRAUN et al., 2000). It is calculated by the Penman-Monteith equation (GREEN & MCNAUGTON, 1997; JONES & TARDIEU, 1998; DRAGONI et al., 2004).

Water consumption of apple trees varies with growing region and year. AUZMENDI et al. (2011) found canopy water requirements of around 630 mm in 2007 and 2008 for Mollerussa, Spain. Apple trees in a lysimeter in Palmerston North, New Zealand were using approximately 4 liters of water per day (BEHBOUDIAN et al., 1998). For Bonn, Germany, per tree water consumption was found to be between 1.8 liters on cloudy days, and 5 liters on sunny days, which equals 0.4 - 1 liters per day per m^2 leaf area (BACKES & BLANKE, 2007). In mild sub-humid climates the water-use rates for sunny days are about 1 to 1.7 liters per day per m^2 leaf area (LAKSO, 2003). Water need during the growing season for apple trees in Germany is supposed to be around 250 to 280 mm (BRAUN, 2008). A general advice is that apple trees in good and deep soils need about 2 liters per tree per day additional to rainfall to maintain sufficient water during dry periods (BRAUN, 2008). Water use is also dependent on crop load (CHEN & LENZ, 1997), especially later in the season (BUWALDA & LENZ, 1992). It is evident that some knowledge about water use of apple trees has been collected through field experiments, but only little information exists for Germany. Overall the single findings have not resulted in a comprehensive understanding of water relations of apple trees.

Apple tree root systems have been found to use the space down to a depth of 1.6 m, with mature trees penetrating to at least 1 m depth (HUGHES & GANDAR, 1993), but no data about rooting depths of developing apple trees is available. Rooting density within the exploited soil volume is generally low. Roots control total tree water use and water status by sensing soil water status and sending a signal to the shoots when soil gets dry (GOWING et al., 1990). This signal was found to consist of high quantities of abscisic acid (ABA), which is then transported to the leaves (DAVIES & ZHANG, 1991). ABA can inhibit stomatal opening and thus reduce water usage of the tree. Apple rootstocks differ in their water conductance and in their exploited soil volume (OLIEN & LAKSO, 1986).

A consequence of water deficit is stress. Water deficit has more dramatic effects on apple trees when it occurs in spring and early summer, than when it takes place later in the season (LAKSO, 2003). Water deficit during flowering in apple can lead to a reduced fruit set and an increased fruit abscission (POWELL, 1974). Water deficit during fruit cell division may reduce cell number (HSIAO, 1973) influence final fruit size and number (KILILI et al., 1996a). Water deficits are known to reduce radial trunk growth (IANCU, 1985). Mid-season water deficit has been found to result in reduced trunk circumference growth and in reduced leaf area and shoot length (MILLS et al., 1996). Late-season water deficit did not reduce shoot growth or total leaf area, but did limit the radial trunk growth, and is thought to have a minimal influence (MILLS et al., 1996). Root growth is less sensitive to water deficits than shoot growth, and the root to shoot ratio of plants generally increases when water availability is limited (ANJUM et al., 2011). The absolute amount of root growth can be reduced under irrigation (LANDSBERG & JONES, 1981), and root distribution is highly affected by irrigation itself and by irrigation management practices (system, timing, and amount) (LEVIN et al., 1979; SOKALSKA et al., 2009).

Intensification of apple orchards, which includes higher numbers of trees per area as well as the use of dwarfing rootstocks that have shallow and sparse root systems, has led to a higher dependence on frequent and adequate water supply. A restriction of water supply significantly reduced total dry weight of apple trees (BUWALDA & LENZ, 1992).

Reductions resulted from reduced dry weights for fruit, leaves, shoots and stems, while root dry weights were not affected. Under very severe water deficit ‘Royal Gala’ apple trees began to show typical signs of extreme water stress: in-rolling of leaves to reduce surface area and death of the main shoot apex (BASSETT et al., 2011). Besides knowledge about water use also some knowledge about effects of water deficits on apple trees is available but has not been used to find general principles that control apple productivity. By connecting and integrating the available knowledge into the MaluSim framework this might be possible. It can also help to identify areas where inadequate knowledge about water relations of apples is available and to focus future research directions.

In many growing regions performance of commercial apple orchards, i.e. fruit size and quality, storability, and long term productivity highly depend on irrigation. But the amount of fresh water available for agricultural use is decreasing worldwide. For an effective irrigation scheduling, a precise adjustment of irrigation amounts to actual plant water consumption is needed to maximize the efficiency of irrigation (CASADESUS et al., 2011; NAOR, 2014). But making decisions on irrigation is complex because it involves many factors (physiological, phenological, meteorological and economical). Each of these factors is subject to uncertainty and the use of plant water stress indicators may enable the grower to precisely adjust irrigation and to compensate for effects of canopy size, application efficiency, and crop load (NAOR, 2006). For many crops it is not necessary to fully irrigate the plants to achieve high yields and several irrigation strategies have been developed. They aim to minimize water use, while maintaining sufficient yields, and reduce environmental problems such as leaching of nutrients and pesticides through the soil to ground water (MILLS et al., 1996). Examples are deficit irrigation (DI), regulated deficit irrigation (RDI) and partial rootzone drying (PRD). PRD is a strategy where water is withheld from one part of the rootzone while another part is well watered. The idea behind it is that a reduced transpiration occurs due to an ABA root-signal derived from the drying rootzone (O'CONNELL & GOODWIN, 2007). DI means to use irrigation at levels below the water use demands of a tree (LAKSO, 2003), while RDI implies the same concept, except for targeting of specific growth stages versus full-season deficits.

Since most experiments were conducted in mature orchards only sparse knowledge about the effects of irrigation during the establishment phase of apple orchards exists. Many trials have been conducted and various irrigation methods evolved, but the underlying knowledge about how much water apple trees need and when, and what happens exactly when they have to deal with water deficits remains not fully understood.

3 MAIN RESEARCH OBJECTIVES OF THIS THESIS

The major objective of this thesis is to provide a universal apple tree model for Europe, which on the one hand can be used for addressing problems in practical applications (e.g. predictions of natural fruit drop or tree thinning response to chemical thinners) and on the other hand can be used for a better theoretical understanding of apple tree behavior under Central-European growing conditions (e.g. understanding effects of additional water supply and water deficits). The final model is not only intended to be a basis for apple orchard management decisions and high quality production in the future, but also for exploring differences between growing regions and for future research, e.g. Climate Change effects on apple orchards and growing sites. For this aim, the MaluSim carbon balance model has been chosen as a basis. The general hypothesis is that, after a parameterization, the model can be used in Europe as a thinning decision support tool and for calculating general carbon balance of apple trees.

Besides the general ability of the MaluSim model to calculate an overall carbon balance and then link this balance to a general thinning status of the trees, the developers also added a specific fruit growth and abscission submodel. This submodel has been based on estimated carbon supply for fruit growth and the relationship between fruit growth rate and abscission, but was not able to correctly calculate final fruit numbers and therefore is still under development. The hypothesis is that by testing and modifying the key relationships and, if required, integrating more available knowledge and relationships on fruit abscission, and, by using accurate weather data, the submodel should be able to calculate an appropriate simulation of natural fruit drop.

There still exist major gaps in our understanding of water relations of apple trees, especially concerning effects of irrigation during the establishment phase and concerning water deficit effects on photosynthesis. One major limitation of the MaluSim model is that water status of the tree is not modeled, but assumed to be non-limiting. A water submodel would not only improve the general carbon balance calculation under a wider range of conditions, but would also enable the user to simulate how water deficits may affect tree and fruit development of apple trees. As a possible future consequence MaluSim could be able to support irrigation management or to decide whether it is useful to install additional irrigation for a particular site. To achieve a universal apple tree model for theoretical and practical applications in Germany and Central-Europe the major hypotheses and derived objectives of this thesis can be summarized as:

I) MaluSim can be used for simulations of carbon balance of apple trees in Germany. To confirm this hypothesis the objectives are:
  - Define a standard tree and parameterize MaluSim for that tree and for weather in Germany. This includes to consider differences in environmental conditions, apple cultivars, and growing systems, and to test the original relationships and assumptions for the prevailing conditions.
  - Run the parameterized model with actual weather data and compare simulation runs with the original model to check if the general behavior of the model is realistic and similar in pattern to original values.

II) By linking carbon balance modeling to general knowledge about fruit development and abscission it will be possible to simulate natural fruit drop and final fruit numbers for a standard apple tree. Therefore, to specifically test and modifiy the fruit growth and abscission submodel of MaluSim, the main objectives are:
  - Examine the original fruit growth and abscission submodel
  - Compare with available literature based knowledge and, if necessary, modify the used relationships of the fruit growth and abscission submodel
  - Compare simulation runs of the modified models with field data on final fruit set of unthinned orchards at different sites in Central-Europe

III) The hypothesis for the field experiment is that by applying additional irrigation under German conditions on a newly planted apple orchard will not only lead to a reliable, but also to a significantly faster and better tree development. Another main objective of the field experiment is to find a relationship between photosynthetic rate and some measure of plant water status. Therefore, the objectives for the field experiment are:
  - Measure the effects of additional irrigation under German conditions in the first years after planting, in comparison to a non-irrigated control treatment
  - Define a relationship between photosynthesis and tree water potential

IV) The last hypothesis is that by using relationships between water status of apple trees and the main processes occurring in apple trees, effects of water deficits on carbon balance can be modeled. The objectives to integrate a water submodel into the MaluSim framework are:
  - Screen available literature about water relations of apple trees and extract relationships
  - Combine and integrate the relationships to develop a water submodel for MaluSim

4 PARAMETERIZATION OF MALUSIM TO GERMAN GROWING SYSTEMS

To be able to use the chosen MaluSim model in Germany, as a first step, the model has to be parameterized to the prevailing conditions. In the original MaluSim model, parameter values are mainly based on summarized data of many apple cultivars from the literature and the studies of Alan N. Lakso and others. The "standard" tree of the original model is a mature slender spindle 'Empire'/M.9 at approximately 2000 trees/ha (LAKSO et al., 2001b). This means that the used input parameter are the ones found in an "average" 'Empire' orchard in New York State, USA. Compared to this, the trees in Germany are much smaller and the planting density is higher with usually about 3000 up to 4000 trees/ha. Another main difference is the used apple variety. In the European Union the main varieties are 'Golden Delicious', 'Gala', 'Pinova', 'Jonagold', 'Braeburn' and some others (STATISTA, 2011).

Additionally to a general parameterization to the location it is necessary to get a "standard" tree for Germany, by counting and measurements of some commercially relevant cultivars in different commercial and research orchards.

4.1 Materials and methods

4.1.1 Modeling

Modeling has been conducted using the auto-programming simulation software STELLA® (Version 9.1.3; isee systems, Lebanon, NH, USA) and MaluSim Version 'MaluSim904LTWthrSt9', which has been supplied by the model developer Alan N. Lakso, Cornell University.

4.1.2 Tree measurements

Tree measurements were conducted in 2012 and 2013 on 5 trees each of 'Fuji', 'Gala', 'Braeburn' and 'Pinova' on the experimental site "Fuchsberg" of Geisenheim University, situated at Geisenheim (49°59'05"N; 7°57'26"E). Additional tree measurements were made in commercial orchards on 8 trees of the cultivar 'Gala' and 8 trees of the cultivar 'Braeburn' at the location Appenheim (49°55'29" N; 8°02'39"E), on 8 trees of the cultivar 'Gala' and 8 trees of the cultivar 'Braeburn' at the location Mainz-Drais (49°58'47" N; 8°11'56"E), and on 20 trees of the cultivar 'Elstar' and 20 trees of the cultivar 'Gala' at the location Zornheim (49°53'42" N; 8°13'08"E).

Counting of total number of flowers, of spurs and of long shoots has been done using a tally counter. For wood surface area calculation, height (in cm), trunk circumference at

35 cm, 80 cm, 130 cm, and 180 cm height above ground, and largest diameter and length of branches has been measured. Height of trees was measured using a folding rule and length of branches and trunk circumference was measured with a measuring tape. Diameter of branches has been measured using a sliding caliper. Wood surface area has been calculated using circumference and height data of the trees and calculating truncated cone or cone (for top segment) surface area (without the top and bottom) for each of the measured segments and adding calculated surface area of the branches. Branches surface area was calculated using the length of the branch and largest diameter with the cone surface formula (without bottom).

4.1.3 Parameterization of MaluSim

While in the USA for commercial apple orchards a moderate density is 2000 trees/ha, in Germany usually around 3000 trees/ha are planted. This makes it necessary to change the ground "area per tree" input. Also the height of the trees is different, with usually 2 to 2.5 m height in Germany, compared to 3 to 4.5 m height in NY State, USA. For the parameterization of MaluSim the latitude is required in the model, to calculate incoming radiation and day length. An apple orchard in Geneva, NY, USA with a latitude of 43° has higher potential mid-summer incoming radiation but a shorter day length than an apple orchard in Geisenheim (latitude 50°) or Germany in general (latitude 48-54°).

To compare simulation runs of the original model with original environmental values to conditions and parameterization for Germany overall six simulation runs were conducted:

1. **USA Wthr USA StT**: For this simulation run the original model with 20-year mean weather data (1971 – 1990) for Geneva, USA, and the original standard tree 'Empire' has been used. Ground area per tree of 5.1 m^2 has not been changed. Latitude of 43° has been used.

2. **USA Wthr GER StT**: For this simulation run the original model with 20-year mean weather data (1971 – 1990) for Geneva, USA, and the new standard tree for Germany has been used. Ground area per tree of 5.1 m^2 has not been changed. Latitude of 43° has been used.

3. **USA Wthr GER StT +AREA**: For this simulation run the original model with 20-year mean weather data (1971 – 1990) for Geneva, USA, the new standard tree for Germany has been used. Ground area per tree has been changed to 3.5 m^2. Latitude of 43° has been used.

4. **GER Wthr USA StT**: For this simulation run the original model with mean weather data of 2012 and 2013 for Geisenheim, Germany, and the original standard tree 'Empire' has been used. Ground area per tree of 5.1 m^2 has not been changed. Latitude of 50° has been used.

5. **GER Wthr GER StT**: For this simulation run the original model with mean weather data of 2012 and 2013 for Geisenheim, Germany, and the new standard tree for Germany has been used. Ground area per tree of 5.1 m^2 has not been changed. Latitude of 50° has been used.

6. **GER Wthr GER StT + AREA**: For this simulation run the original model with mean weather data of 2012 and 2013 for Geisenheim, Germany, and the new standard tree for Germany has been used. Ground area per tree has been changed to 3.5 m^2. Latitude of 50° has been used.

4.2 Results

4.2.1 Parameterization of MaluSim – a standard tree for Germany

Results of the tree measurements to achieve data for a MaluSim standard tree for Germany, compared to the original standard tree, are presented in Table 1.

Table 1: Counted numbers of flowers, long shoots and spurs, and measured wood surface area (m^2) for 'Gala', 'Braeburn', 'Fuji', 'Pinova', and 'Elstar' in comparison to numbers used in the original MaluSim model for 'Empire'. The additional column "1/3" stands for one third of the original standard tree. "Overall" values are calculated by using the average values of the cultivars 'Gala', 'Braeburn', 'Fuji', 'Pinova', and 'Elstar'. "Overall (–Elstar)" has been added because 'Elstar' showed very dissimilar values compared to 'Gala', 'Braeburn', 'Fuji', 'Pinova', who did not differ much between each other.

Name	Original	"1/3"	Gala	Braeburn	Fuji	Pinova	Elstar	Overall	Overall
Variety	*Empire*		*Gala*	*Braeburn*	*Fuji*	*Pinova*	*Elstar*		*(-Elstar)*
# flowers	2400	800	719	834	768	773	427	704	774
# long shoots	194	65	69	83	74	60	117	81	71
# spurs	686	229	234	303	266	254	207	253	264
Wood SA	1.5	0.5	0.5	0.51	0.5	0.48	0.55	0.51	0.50

There exist differences between apple cultivars in Germany, but besides 'Elstar', all other chosen cultivars did not differ very much in the current case. For this reason 'Elstar' values were excluded and "Overall (-Elstar)" values were used for the standard tree for Germany. Compared to the original standard 'Empire' tree, apple trees in Germany are much smaller and comparable to values of about one third of the original standard ones (see Table 1, column: "1/3").

4.2.2 Test of parameterization - Comparison of simulation runs for USA and Germany

Daily canopy photosynthesis with 20-year mean weather data (1971-1990) of Geneva, USA is simulated to increase after bud break, reaching its maximum values between 60 and 130 days after bud break (DABB), followed by a decrease until 206 DABB (Figure 3).

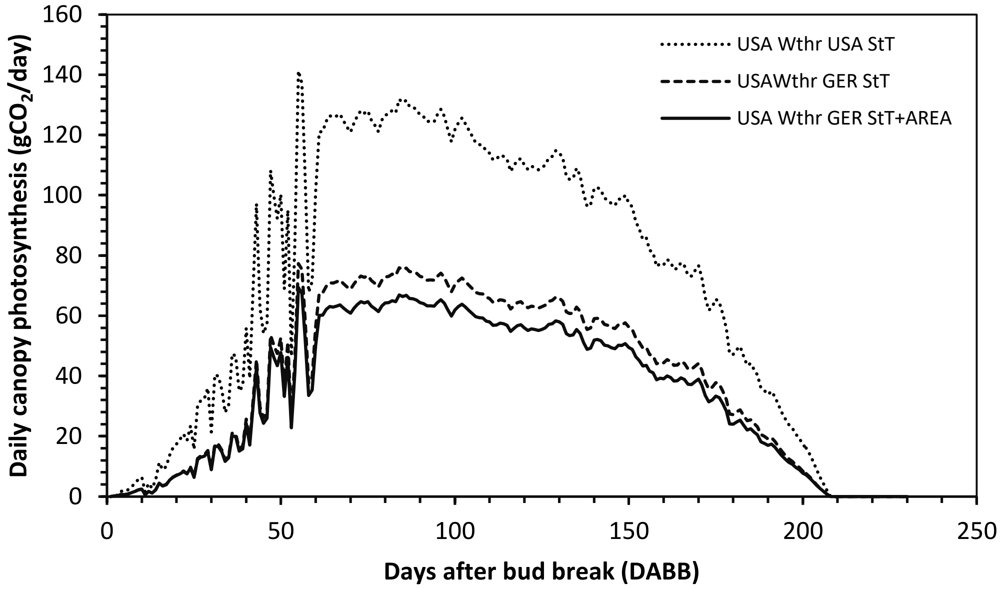

Figure 3: Simulated daily canopy photosynthesis of modeled 'Empire' standard trees (USA Wthr USA StT- dotted line), of modeled German standard trees with an area per tree of 5.1 m^2 (USA Wthr GER StT – dashed line), and of modeled German standard trees with an area per tree of 3.5 m^2 (USA Wthr GER StT+AREA- solid line), using long-term weather data of Geneva, USA.

During most of the season, simulated daily canopy photosynthesis of modeled 'Empire' standard trees is calculated to be about twice as high as the one of modeled German standard trees with a ground area per tree of 3.5 m^2. Values of modeled German standard trees with an area per tree of 5.1 m^2 are about 15 % higher than the ones modeled with an area per tree of 3.5 m^2. Seasonal cumulative canopy photosynthesis was simulated to be 15.9, 8.9 and 7.9 kg of fixed CO_2 per tree for 'USA Wthr USA StT', 'USA Wthr GER StT' and 'USA Wthr GER StT+AREA', respectively. Net cumulative CO_2 fixation (photosynthesis minus respiratory losses) per tree per season was simulated to be 13.3, 7.9 and 6.9 kg/tree for 'USA Wthr USA StT', 'USA Wthr GER StT' and 'USA Wthr GER StT+AREA', respectively.

Results of simulation runs with two-year average weather data (2012-2013) of Geisenheim, Germany are shown in Figure 4.

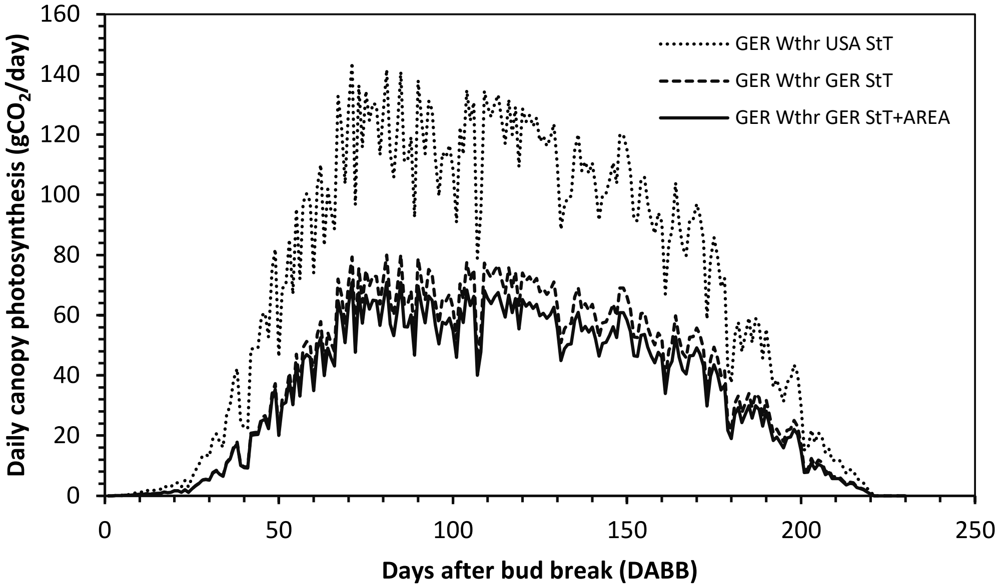

Figure 4: Simulated daily canopy photosynthesis of modeled 'Empire' standard trees (GER Wthr USA StT- dotted line), of modeled German standard trees with an area per tree of 5.1 m^2 (GER Wthr GER StT – dashed line), and of modeled German standard trees with an area per tree of 3.5 m^2 (GER Wthr GER StT+AREA- solid line), using two-year mean weather data of 2012 and 2013 from Geisenheim, Germany.

Modeled daily canopy photosynthesis with German weather shows in general a similar course as with USA weather. It is simulated to increase after bud break reaching maximum values between 66 and 148 DABB and followed by a decrease until 219 DABB. Simulated length of season is about two weeks longer in Germany than in the USA (Figure 3; Figure 4). Seasonal cumulative canopy photosynthesis using German weather data only differed by 0.1 kg from simulation runs using weather data of Geneva USA and was simulated to be 15.8, 8.8 and 7.8 kg of fixed CO_2 per tree for 'GER Wthr USA StT', 'GER Wthr GER StT' and 'GER Wthr GER StT+AREA', respectively. Net cumulative CO_2 fixation per tree per season was simulated to be the same as for USA (see above).

4.3 Discussion

When comparing simulation runs using the 'Empire' standard tree with Geneva and Geisenheim data, it becomes evident that, overall, weather data was comparable between sites. Although modeled season length is slightly longer for Geisenheim (10 days) than for Geneva, total seasonal cumulative canopy photosynthesis is similar. This result is in contrast to published simulation runs for New Zealand, where a longer growing season led to a higher amount of total seasonal cumulative canopy photosynthesis compared to simulation runs for Geneva, NY, USA (LAKSO et al., 2001b). But simulated season for New Zealand was about 60 days longer than for Geneva and also showed higher photosynthesis values than for Geneva in mid-season (100 to 180 DABB), probably caused by higher incoming radiation in New Zealand compared to Geneva, NY. Another main change for parameterization was latitude. While simulation runs for New Zealand were based on latitude of 40°, and simulation runs for Geneva, USA on latitude of 43°, Geisenheim is situated at latitude of 50°. Higher latitude leads to a longer day length during the season, but also to a lower incoming radiation during the day. But light interception (LI) calculations of PALMER (1989b) indicate that maximum possible % LI is not very different for 51.3° and 40° from June to September. This agrees with the presented simulations, where no relevant differences were obtained.

MaluSim appears to be a valuable tool for comparing different apple growing sites (ROBINSON & LAKSO, 2011) and regions (LAKSO et al., 2001b), which is additionally supported by the presented simulation runs. This also makes it a possible tool to identify valuable as well as unsuitable growing sites without the need to conduct practical trials. Additionally it can be used to compare orchards of different productivity and to understand potential differences. Overall, it was possible to parameterize MaluSim to a more typical tree and for German growing conditions. Parameterization-simulation runs indicate that MaluSim, using the original as well as the new German standard tree, is in general realistic. Measured input parameter for the new German standard tree were in a range of about 33 % of the original 'Empire' tree input parameter, but daily canopy photosynthesis has been calculated to be about 50 % of the original. The same has been found for seasonal cumulative canopy photosynthesis. Dense trees have a high total LI but usually high internal shading occurs. LI of apple trees is known to depend on the height of trees, but also on tree architecture, and on the particular training and planting system (JACKSON, 1980). Especially within-tree shading can have a high effect on LI (WILLAUME et al., 2004). For smaller trees less internal shading is likely to occur, which leads to a comparatively higher LI (lower total LI than for dense trees, but most leaves are supposed to have good light conditions) and thus a lower reduction of total canopy photosynthesis per m^2. Through the lower active leaf area per area per tree, a lower LAI is calculated. Additionally, through the use of an exponential function in the photosynthesis calculation, a reduction to half total canopy photosynthesis is calculated.

With the parameterization and the new standard tree it is possible to estimate carbon balances for Germany. Commercial apple orchards in Central-Europe do not differ much compared to German orchards. Therefore, the parameterized model can also be used to make simulation runs for apple orchards in Central-Europe.

5 THINNING AND NATURAL FRUIT DROP – TESTING AND IMPROVING MALUSIM FOR NATURAL FRUIT DROP SIMULATIONS

The fruit growth and abscission submodel (see chapter 2.2.2.5 and 2.3.4) of MaluSim was expected to provide useful information about thinning status and natural fruit drop for trees in Germany after its parameterization. Following the initial parameterization, simulation runs using the submodel were conducted, but it has not been able to adequately simulate realistic tree behavior in terms of natural fruit drop and final fruit number calculation. It was too sensitive and with only a slight carbon deficit it simulated that all fruits will drop. This problem has also been confirmed for using MaluSim in the USA and is one reason why the submodel has not been used for grower support (LAKSO, 2012).

In general, it should be possible to correctly simulate natural fruit drop and final fruit numbers for a standard apple tree, when the used relationships of the submodel are correct and include all relevant aspects concerning fruit development of abscission in apples.

5.1 Materials and methods

5.1.1 Modeling

The following modifications have been conducted using the auto-programming simulation software STELLA® (Version 9.1.3; isee systems, Lebanon, NH, USA). All modified models are based on MaluSim Version 'MaluSim904LTWthrSt9' provided by A. Lakso, Cornell University.

5.1.2 Parameterization to Zornheim and modifications of the fruit submodel

Experimental data of the Master-Thesis of Theresa M. Pfeifer (conducted in 2012) were used as a test. At first, a parameterization of the model to the location Zornheim, Germany has been made (using weather data of Zornheim and latitude of 50°). Then the default fruit growth and abscission submodel was applied and simulation runs showed an oversensitive behavior and calculated that all fruits will drop, which did not occur in the field experiments. Further on, data of field measurements (see Table 2) has been integrated to incorporate the exact parameter of the trees. Additionally to tree data, a pollination factor of 0.334 was used, which has been calculated from numbers of flowers during full bloom and numbers of fruitlets counted after unpollinated flowers have dropped. This meant that 33.4 % of the flowers were not pollinated.

Table 2: Input parameter of the original MaluSim model and changed input parameter used to test the fruit submodel based on a field experiment with 'Gala', conducted at the location Zornheim, Germany. Used field tree data is the average of 10 measured trees.

	Original MaluSim	Field data of 'Gala'
Latitude	*43°*	50°
Weather data	*Geneva, NY, USA*	Zornheim, Germany
Bud break (DOY)	*105*	84
Initial number of flowers	*2400*	727
Number of long shoots	*194*	82
Number of spurs	*686*	229
Wood surface area (m^2)	*1.5*	0.45
Pollination factor	*0*	0.334

Because simulation runs using the presented values also resulted in a calculated drop of all fruits, modifications of the submodel were conducted. Several different modified fruit growth and abscission submodels based on published data (CORELLI-GRAPPADELLI et al., 1994; STANLEY et al., 2000; LAKSO et al., 2001b; LAKSO et al., 2006a; DÖRFLINGER, 2010; GREENE et al., 2013) and field measurements conducted at the locations Geisenheim and Zornheim, were generated.

Overall, the following parameter were tested according to their influence on model performance: pollination factor, timing of non-pollinated fruitlet drop, start of fruit abscission caused by carbon deficit, calculated time of full bloom, fruit abscission curve, initial fruit weight, and three to five day fruit CO_2 accumulator. Only the most interesting modifications are presented in the following.

The modification (G4-4) that obtained best results in the tests is described at first. Additionally, some other modified submodels are displayed to show how changes of parameter affect submodel performance and to compare results.

For model 'G4-4' the fruit abscission curve has been modified to 'Gala', a common cultivar in Europe, by incorporating the measured fruit abscission curve of 'Gala' (Figure 5), published by LAKSO et al. (2001b). Additionally, simulation runs using the abscission curve of 'Empire' (E4-4) and 'Delicious' (D4-4) were made and compared to field data.

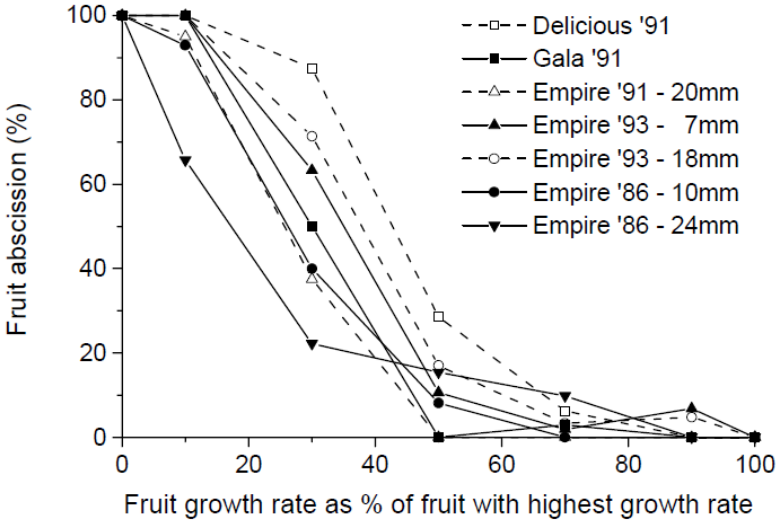

Figure 5: Relationship between fruit abscission and fruit growth rate as % of the fastest growing fruit in a population in several NAA or shade studies. (Figure from LAKSO et al., 2001b)

In the original model, fruit drop caused by carbon deficit is supposed to start at full bloom. This caused the calculation of an early drop of all flowers in the tests and therefore has been modified. Modified models, starting fruit drop by carbon deficit calculation on 200 (G4-2), 250 (G4-3), 300 (G4-4), and 350 (G4-5) accumulated growing degree days, are displayed for ‘Gala’ abscission curve. For ‘Empire’ abscission curve, modified models for 300 (E4-4), 350 (E4-5), 400 (E4-6) and 420 (E4-6b) accumulated growing degree days, and for ‘Delicious’ 300 (D4-4) and 350 (D4-5) accumulated growing degree days, are shown.

For the timing of non-pollinated fruitlet drop best results were obtained when using a recommendation of the original model of 300 accumulated growing degree days. Additionally, the model assumes 190 accumulated growing degree days to be the day of full bloom, which corresponded well with conducted field observations. Changes of initial fruit weight did not lead to improved results and thus was kept as in the original model. To avoid fruit drop calculation accounted by short time changes of carbon balance a CO_2 accumulator for usually three to five days is used. Most realistic simulations of natural fruit drop were obtained using a 4-day CO_2 accumulator.

An overview of the presented modifications can be found in Table 3. Parameter used for modified models are: pollination factor (PollFctr), drop of unpollinated flowers (UnpullFlDrop), x-day average CO2 accumulator (CO2Acc), fruit abscission curve (FrtAbscC), and start of carbon caused fruit abscission (CarbCFrtAbscSt).

Table 3: Overview of parameter values used in the presented modifications of the fruit submodel.

Model name	*G4-2*	*G4-3*	*G4-4*	*G4-5*	*E4-4*	*E4-5*	*E4-6*	*E4-6b*	*D4-4*	*D4-5*
PollFctr	*0.334*	*0.334*	*0.334*	*0.334*	*0.334*	*0.334*	*0.334*	*0.334*	*0.334*	*0.334*
UnpollFlDrop	*300*	*300*	*300*	*300*	*300*	*300*	*300*	*300*	*300*	*300*
CO2Acc	*4*	*4*	*4*	*4*	*4*	*4*	*4*	*4*	*4*	*4*
FrtAbscC	*Gala*	*Gala*	*Gala*	*Gala*	*Empire*	*Empire*	*Empire*	*Empire*	*Delicious*	*Delicious*
CarbCFrtAbscSt	*200*	*250*	*300*	*350*	*300*	*350*	*400*	*420*	*300*	*350*

In the first step of testing the modified models simulated final fruit numbers were compared to counted fruit numbers of the location Zornheim, where final fruit numbers following natural fruit drop, without any additional thinning, have been recorded.

5.1.3 External validation for the locations Jork (Germany), and Wädenswil, Lindau and Güttingen (Switzerland)

Further on, the modified models were tested for the location Jork in Germany (field data of 'Elstar', 'Kanzi', and 'Braeburn', from 2010 to 2012, ESTEBURG Obstbauzentrum Jork), and for the locations Wädenswil, Lindau and Güttingen in Switzerland (field data of 2012, research center Agroscope Wädenswil). The field data of unthinned control treatments has been supplied by Michael Clever for the location Jork, and by Michael Gölles and Simon Schweizer for locations in Switzerland.

For tests of the models for the location Jork only latitude and weather data of Jork has been used, all other parameter were set as described for the location Zornheim. For tests of the models in Switzerland, two different simulation runs are presented, one with changed latitude and weather data (all other parameter of the location Zornheim), and one with changed latitude, weather data and number of flowers of the experimental trees (all other parameter of the location Zornheim).

5.2 Comparisons of natural fruit drop simulation to actual field data

5.2.1 Zornheim, Germany (2012)

Initial fruit number of 727 fruits steeply declines on DABB 47 (start of carbon balance based fruit abscission and day of unpollinated fruit drop reduction) and 48 (Figure 6). After this point only a slight decline from 265 down to 237 fruits is calculated between DABB 56 to 62. No further reduction of fruit numbers is calculated after DABB 62. All calculated fruit reductions correspond to a negative carbon balance of about -20 g/day or lower.

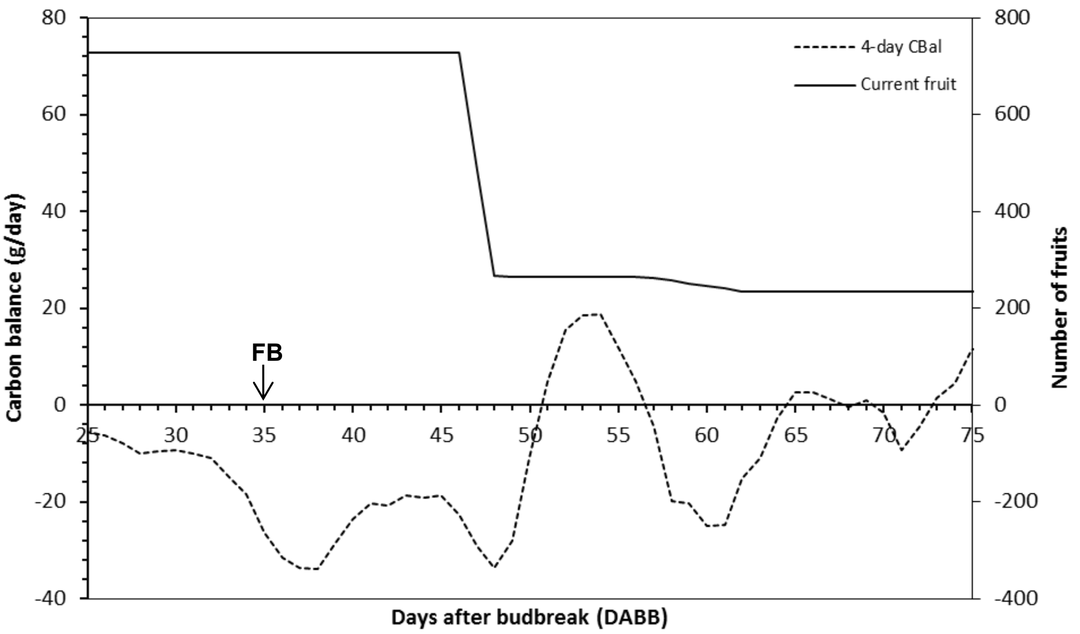

Figure 6: Calculated 4-day average supply-demand balance (black dashed) and fruit numbers (black line) for the cultivar 'Gala' at the location Zornheim, 2012 using the best performing modification 'G4-4' in which the fruit are not sensitive to carbon balance until 300 accumulated growing degree days. Day of full bloom was recorded in the orchard on 35 DABB.

Simulation runs for Zornheim using modifications 'G4-4', 'E4-6' and 'E4-6b' showed the best results of final fruit numbers with low deviations of 0, 2.1, and 1.7 %, respectively (Table 4). In addition, 'E4-5' had a slightly higher deviation of 4.2 %, which equals a difference of 10 fruits to the target number. Compared to this, high deviations were calculated for the models 'G4-2' and 'D4-4', with 100 and 72.2 %, respectively.

Table 4: Observed (Obs.) fruit numbers for the location Zornheim (Zo), 2012 and calculated fruit numbers (# fruits) of the modified MaluSim models G4-2 to D4-5, including deviation in fruit numbers (Δ fruits) and percent (% deviation).

Site, year	**Obs.**		G4-2	G4-3	G4-4	G4-5	E4-4	E4-5	E4-6	E4-6b	D4-4	D4-5
Zo, 2012	**237**	*# fruits*	0	162	237	293	165	227	232	241	66	155
		Δ fruits	*-237*	*-75*	*0*	*56*	*-72*	*-10*	*-5*	*4*	*-171*	-82
		% deviation	*100.0*	*31.6*	*0.0*	*23.6*	*30.4*	*4.2*	*2.1*	*1.7*	*72.2*	34.6

5.2.2 Jork, Germany (2010-2012)

For 2010, lowest deviation was obtained again by model 'G4-4', with a deviation of 1 fruit (0.5 %) (Table 5). In addition, 'E4-6' and 'E-4-6b' showed low deviations of 3 and 7 %, respectively. Highest deviations from target fruit numbers occurred in simulations of 'D4-4' and 'G4-3', with deviations of 88 (43.8 %) and 76 (37. 8%) calculated fruits. In 2011 a late frost occurred after bloom. Since MaluSim does not model frost it is not useful to test against such conditions and the data has been omitted.

Table 5: Observed (Obs.) and calculated fruit numbers (# fruits) for the location Jork (Jo) 2010 and 2012, with deviations in fruit numbers (Δ fruits) and percent (% deviation).

Site, year	**Obs.**		G4-2	G4-3	G4-4	G4-5	E4-4	E4-5	E4-6	E4-6b	D4-4	D4-5
Jo, 2010	**201**	*# fruits*	132	125	202	231	153	181	195	187	113	142
		Δ fruits	*-69*	*-76*	*1*	*30*	*-48*	*-20*	*-6*	*-14*	*-88*	*-59*
		% deviation	*34.3*	*37.8*	*0.5*	*14.9*	*23.9*	*10.0*	*3.0*	*7.0*	*43.8*	29.4
Jo, 2012	**139**	*# fruits*	119	148	149	220	65	162	400	417	30	56
		Δ fruits	*-20*	*9*	*10*	*81*	*-74*	*23*	*261*	*278*	*-109*	*-83*
		% deviation	*14.4*	*6.5*	*7.2*	*58.3*	*53.2*	*16.5*	*187.8*	*200.0*	*78.4*	59.7

In Jork 2012 the model ‘G4-3’ and ‘G4-4’ showed lowest deviations, with a deviation of 9 (6.5 %) and 10 (7.2 %) fruits respectively, while the other models that performed well in Jork for 2010 and in Zornheim for 2012, ‘E4-6b’ and ‘E4-6’ had very high deviations of 200 and 187.8 %, respectively.

5.2.3 Güttingen, Lindau and Wädenswil, Switzerland (2012)

In Wädenswil in 2012 also a late frost occurred, which leads to the same problems as described above for the simulation runs of Jork, 2011 and data has been omitted. For the location Güttingen, using fruit numbers of Zornheim, model ‘E4-6b’ achieved the lowest deviation of 0.4 % followed by ‘E4-6’ and ‘G4-4’, while model ‘G4-2’ had the highest deviation of 217 fruits (78.3 %) (Table 6.). When using the counted numbers of Güttingen, model ‘E4-6’ showed the lowest deviation of 15 fruits (5.4 %), followed by ‘G4-4’ with 9.4 % deviation (26 fruits). Again model ‘G4-2’ had the highest deviation of 83.8 %.

Table 6: Observed (Obs.) and calculated fruit numbers (# fruits) for experimental sites in Switzerland (Güttingen (Gü) and Lindau (Li)). Simulation runs for each site with 727 initial flowers (bold) and with counted initial flower numbers (# fl), including deviations in fruit numbers (Δ fruits) and percent (% deviation).

Site, year	**Obs.**		G4-2	G4-3	G4-4	G4-5	E4-4	E4-5	E4-6	E4-6b	D4-4	D4-5
Gü, 2012	**277**	*# fruits*	60	139	250	314	189	227	260	276	111	138
		Δ fruits	*-217*	*-138*	*-27*	*37*	*-88*	*-50*	*-17*	*-1*	*-166*	*-139*
		% deviation	*78.3*	*49.8*	*9.7*	*13.4*	*31.8*	*18.1*	*6.1*	*0.4*	*59.9*	50.2
# fl 1666	**277**	*# fruits*	45	136	303	322	218	225	262	235	77	82
		Δ fruits	*-232*	*-141*	*26*	*45*	*-59*	*-52*	*-15*	*-42*	*-200*	*-195*
		% deviation	*83.8*	*50.9*	*9.4*	*16.2*	*21.3*	*18.8*	*5.4*	*15.2*	*72.2*	70.4
Li, 2012	**196**	*# fruits*	6	76	186	198	123	133	161	163	43	64
		Δ fruits	*-190*	*-120*	*-10*	*2*	*-73*	*-63*	*-35*	*-33*	*-153*	*-132*
		% deviation	*96.9*	*61.2*	*5.1*	*1.0*	*37.2*	*32.1*	*17.9*	*16.8*	*78.1*	67.3
# fl 1646	**196**	*# fruits*	0	79	193	211	104	136	157	90	33	50
		Δ fruits	*-196*	*-117*	*-3*	*15*	*-92*	*-60*	*-39*	*-106*	*-163*	*-146*
		% deviation	*100.0*	*59.7*	*1.5*	*7.7*	*46.9*	*30.6*	*19.9*	*54.1*	*83.2*	74.5

For the location Lindau, using fruit numbers of the location Zornheim and of the location Lindau, model ‘G4-2’ had the highest deviations of 96.9 and 100 %. In contrast, model ‘G4-5’ and again ‘G4-4’ obtained the lowest deviations for simulation runs for Lindau, with 1.0 and 7.7 % (with Zornheim flower numbers), and with 5.1 and 1.5 % (with Lindau flower numbers), respectively.

5.2.4 Overall performance of the modifications

Overall, ‘G4-4’ showed a very low total deviation of 4.8 %, followed by ‘E4-5’ with a total deviation of 18.6 %. Taking out additionally simulation runs of Switzerland, where flower data of Zornheim and not of the locations in Switzerland has been used, overall deviation of ‘G4-4’ is 3.7 %, while all other modified models showed total deviations of over 15 %.

5.3 Discussion

The modification ‘G4-4’ of the MaluSim fruit growth and abscission submodel showed very good results of final fruit number calculation in comparison to observed fruit numbers of unthinned orchards. With this modification it was possible to correctly estimate final fruit numbers for several sites and different years with low variance. One problem with the approach of adjusting factors to find the best fit to a dataset, and not being based on a biological basis, is that it can make predictions in other conditions more incorrect although this was not the case for the data of Jork and Switzerland. But this problem is likely to occur when the modification is used under conditions that differ much more to the ones in Zornheim. Therefore, the modification should be tested against more independent data and the underlying biological relationships should be included as soon as they are fully understood.

One main point that has been modified compared to the original model was the fruit abscission curve. Simulation runs using the abscission curves of ‘Gala’, ‘Empire’ and of ‘Delicious’ were presented in this thesis. A modified model of ‘Gala’ showed in general the best agreement with field data (model ‘G4-4’) which supports the hypothesis, that ‘Gala’ is a good standard for European cultivars, since field data of several cultivars has been used for comparisons. Some modified models of ‘Empire’ also showed good results for some simulation runs, while modified models of ‘Delicious’ did not show satisfactory results. When comparing the abscission curves used for ‘Delicious’ with the ones for ‘Gala’ or ‘Empire’ the main difference is that for ‘Delicious’ fruits are calculated to be abscised between 0 and 80 % of maximum fruit growth rate. This has also been confirmed by similar abscission patterns found for ‘Delicious’ by GREENE et al. (2013). For ‘Gala’, fruits are only calculated to be abscised between 0 and 50 % of maximum fruit growth rate.

By growth rates over 50 % of maximum fruit growth, fruits are expected to remain on the tree. ‘Empire’ abscission is in between but closer to ‘Gala’, with a range from 0 to 60 %. This main difference has led to better predictions of models using ‘Gala’ and ‘Empire’ abscission curves than for the ones using ‘Delicious’ abscission curves. The used abscission pattern for ‘Gala’ is in between the simplified model and the actual model of GREENE et al. (2013), while most published studies show a pattern of actual fruit drop comparable to the one used for ‘Delicious’ (LAKSO et al., 2001a; GREENE et al., 2005; LAKSO et al., 2006a; GREENE et al., 2013; SCHWEIZER et al., 2014). But most studies, that relate abscission to maximum fruit growth rate, were conducted with chemical thinners, which may have altered natural fruit abscission pattern. Interestingly, SCHWEIZER et al. (2014) showed that in many cases fruits that were supposed to drop according to their growth rate compared to the maximum fruit growth rate remained on the tree, while others, that were supposed to stay on the tree, dropped, but overall numbers were mainly correct. This supposes that other factors, additional to maximum fruit growth rate, are involved in the fruit abscission process. Possible other influencing factors are for example pollination effectiveness or other stresses (frost, nutrient or water stress).

Besides varying fruit abscission curves, the time interval where carbon balance induced fruit drop can occur has been changed in the modified models. In the original model it started with the day of full bloom. Tested models using this early date, showed an oversensitive calculation of fruit drop (see results of ‘G4-2’), even when carbon to fruit accumulator was set up to 5 days of buffering. Best results were obtained when start of carbon balance induced fruit drop was set to a point in between 300 and 350 accumulated growing degree days, which corresponds to about 10 to 14 days after full bloom and a fruit diameter of 7-9 mm. For the ‘Gala’ abscission curve, best results were obtained using 300 accumulated growing degree days as a switching point. This implies that either, something in the early carbon balance calculation of the model is wrong or insufficient, or that at this time fruit are not sensitive to the general carbon balance for fruit drop or retention of fruit and other factors might have a higher influence at this time. BYERS et al. (1990b) found that shading from 5 to 15 DAFB led to less heavy fruit drop than later shading (up to about 40 DAFB), which indicates that fruits are less sensitive at that time or that carbon need of fruits is very low at the beginning. The study of CORELLI-GRAPPADELLI et al. (1994) of carbon allocation after bloom showed that the carbon for fruit development immediately after bloom came from nearby spur leaves. It remains unclear which are the main factors and relationships during early flower and fruit development. In the current case a single switching point from zero sensitivity to being fully sensitive is used, which is not very likely to represent realistic behavior. In reality, rarely a sharp change in any physiological parameter occurs. A better approach would be to use a mechanistic relationship which includes all relevant factors. But these relationships are not fully understood and described. For the presented simulations with only final fruit number comparison, using the simple approach led to very sufficient results.

Most thinning studies start fruit measurements on 10 or 15 DAFB and little is known about very early time of fruit development. Fruitlet growth mainly is recorded starting from about 8-9 mm diameter (LAKSO et al., 1995) when reliable measurements are possible. Additionally, in the traditional sensitivity pattern of chemical thinning responses it has been found that thinning effect at petal fall is lowest (ROBINSON & LAKSO, 2011), which also indicates that shortly after bloom other factors support fruit development or inhibit abscission. Other possible main factors during the early development of apple fruits are hormones (e.g. auxin (GREENE, 2006)), pollination and fertilization (DENNIS, 2003), and also seed development (BERÜTER & DROZ, 1991; ABRUZZESE et al., 1995) and number (HANDSCHACK, 1997). It is unknown how exactly and how long these factors influence the abscission process.

Using initial flower numbers counted in Güttingen and Lindau only slightly improved simulation results compared to using fruit numbers of the location Zornheim. This can be explained by the daily adjustment of fruit numbers to a level the tree is capable to support as soon as the carbon balance drop calculations is switched on. The differences in initial flower numbers might be linked to a general differing tree size, and in general, an exact parameterization to conditions in Switzerland should give best simulation results. But simulations showed good to very good results and trees are presumably similar or only slightly bigger than the ones in Zornheim.

All presented tests were performed for data of the past. For practical reasons an early season forecast of final fruit set would be very desirable. The conducted simulation runs using the fruit submodel of MaluSim indicate that this is not possible, because the prevailing conditions during the season affect fruit set and drop. Besides MaluSim, some other methods are under testing for their ability to become a good thinning advice tool or to predict natural fruit drop. An example is the one by GREENE et al. (2005; 2008; 2013), which is a tool based on a similar fruit abscission-to-growth rate relationship to estimate thinning efficiency after the thinning spray has been applied. The method by GREENE has also been developed in the USA and then was tested in Europe with medium to good success (GÖLLES & WIDMER, 2012). But a detailed analysis of tests that were conducted at different sites in Switzerland, Italy, Austria and Germany, from 2007 until 2013, indicated that a reliable final forecast of how many fruits will retain and how many will fall off the tree was not possible using the method of GREENE (SCHWEIZER et al., 2014), since total fruit drop is not determined at a specific date. Another method, which has been tested for forecasting fruit drop, is near infrared spectroscopy (NIRS) measurement of fruitlets, but this technique was also only able to explain fruit drop afterwards and not beforehand (SCHWEIZER et al., 2014). These results support the hypothesis that an early season forecast of final fruit set is not possible, because seasonal weather is the main factor. This was also pointed out by simulation runs of MaluSim.

Although an early season forecast is not possible, it is possible with MaluSim to calculate actual carbon balance, and it is also even possible to calculate future carbon balance for the next days by using weather forecast data. Reliability of the model for predicting carbon balances in the future then highly depends on the reliability of the forecasted weather data. Temperature forecasts are often acceptable four to five days in advance, but critical radiation forecasts are often poor as cloud-cover is difficult to predict and there is little demand for radiation forecasts beyond overcast, partly cloudy or sunny.

The method used in the USA of estimating the balance between total carbon supply to total demand appears to be a good way to use MaluSim for helping growers making thinning decisions in the USA (LAKSO et al., 2006b; LAKSO, 2011). But in general, a reliably working fruit growth and abscission submodel should be able to improve model predictions. Carbon balance and available carbon to fruit depends on actual fruit numbers. Using a fixed fruit number during the whole season leads to an at least slightly wrong simulation of carbon balance and partitioning.

Overall, the modified model ‘G4-4’ led to very reasonable results with very good calculations of final fruit numbers. No other known model is able to achieve a comparable quality of calculation. This makes it a very promising tool but the modified fruit growth and abscission submodel should still be tested against other independent data, if available against dynamic fruit drop data and not only with final fruit numbers. In addition it should also be tested for its ability to understand extraordinary thinning events of the past, as well as to provide real-time simulations of carbon balances for the current season.

6 WATER RELATIONS AND GAS EXCHANGE OF APPLE TREES: EFFECTS OF ADDITIONAL IRRIGATION ON A NEWLY PLANTED APPLE ORCHARD

There still exist major gaps in the understanding of water relations of apple trees, especially concerning effects during the establishment phase and concerning water deficit effects on photosynthesis. Most previous studies concentrate on irrigation effects on mature trees and in warmer regions. For this reason a field experiment was conducted to describe effects of additional irrigation on newly planted apple trees in Germany and to explore the relationships between water status and photosynthesis.

6.1 Materials and methods

6.1.1 Experimental site and plant material

The study was carried out during 2012 and 2013 at an experimental orchard of Geisenheim University, situated in Geisenheim, Germany (49°59’06’’ N; 7°56’43’’ E; 95 m a.s.l.). Apple trees of three different cultivars (*Malus* x *domestica* Borkh.) were planted in autumn of 2011. ‘Jugala’ (small fruit size), and ‘AW106’ (‘Sapora®’ referred to as ‘Sapora’; big fruit size), were each grafted on M.9 rootstock, while ‘Fresco’ (‘Wellant®’ referred to as ‘Wellant’; mid-size fruits) was grafted on ‘Summerred’ as an interstock and M.9 as a rootstock. Planting density was 3125 trees/ha (1 x 3.2 m) without headland and trees were trained as thin slender spindles. The experimental plot consisted of 9 rows with 85 trees each (765 total trees), with blocks of 14 to 15 trees. A randomized plot design with 5 replications per cultivar and treatment has been used. Three different irrigation treatments were applied from bloom to end of august (to achieve stop of long shoot growth and inhibit regrowth of terminated shoots) in 2012 and 2013:

CT → Control treatment was only rain fed and no additional irrigation has been applied.

ET → Evapotranspiration treatment has been rain fed and additional irrigation has been applied according to a water balance calculation. Crop evapotranspiration (ET_c) has been calculated using a reference evapotranspiration (ET_o) multiplied with a crop coefficient (kc) (→ $ET_c = ET_o * k_c$) (ALLEN et al., 1998). ET_o has been provided by DWD (Deutscher Wetter Dienst - German weather service) situated in Geisenheim. Irrigation was calculated using ET_o, daily rainfall amounts and a k_c of 0.5. This is based on that 50 % of the evapotranspiration is used by the trees, and 50 % is used by the grass in between the rows (BRAUN, 2012). A k_c of 0.5 is supposed to be sufficient for developing apple orchards until mid-season and leading to minor water deficits from mid-season to late-season (IMMIK, 2008). ET irrigation was applied with drip lines (dripper every 30 cm; with 1 dripper dripping 1.61 L/h --> 5.33333 L/m/h; NETAFIM UNIRAM 20012 AS) when calculated water deficit was higher than 15 liters per tree.

NT → Normal treatment has been rain fed and additionally irrigated with 2 L/tree/day (usually irrigated 2 times per week 7 liters). This irrigation has been based on a general advice for additional irrigation in Germany. NT has not been irrigated when precipitation of the previous week was higher than 25 mm. In this treatment single drippers were used (1 dripper per tree; 2 L per h; NETAFIM CNL junior dripper).

Meteorological data (precipitation, global radiation, photosynthetic active radiation, and temperature) was obtained using a weather station situated directly beside the orchard (2 m distance). Canopy management practices, fertilization and pruning were carried out following standard commercial practices for apple orchards.

6.1.2 Phenology and tree descriptions

Phenological stages of tree development in 2012 and 2013 were classified according to the BBCH scale (MEIER, 2001). Monitored stages were BBCH 07 (beginning of bud break: first green leaf tips just visible), BBCH 53 (bud burst: green leaf tips enclosing flowers visible), BBCH 54 (mouse-ear stage), BBCH 55 (flower buds visible (still closed)), BBCH 57 (pink bud stage), BBCH 60 (first flowers open), and BBCH 65 (full bloom).

Tree measurements were performed several times during the experiment. Counting has been done using a tally counter. Total number of flowers per tree has been counted during flowering time on 24 trees per treatment in 2012, and on 48 trees per treatment in 2013. Number of spurs was counted on 24 trees per treatment, in May 2012 and in July 2013. Number of long shoots has been counted on the same 24 trees like the spur counting in October 2012 and at the end of July 2013. In 2012, 12 long shoots per treatment were tagged and length was measured weekly until shoot cessation. This has been done for 24 long shoots per treatment in 2013. After shoot cessation in 2012 and 2013, shoot length of all new long shoots of 12 trees per treatment was measured. For wood surface area calculation, height (in cm), trunk circumference at 35 cm, 80 cm, 130 cm, and 180 cm height above ground, and largest diameter and length of branches was measured on 12 trees per treatment. Height of trees was measured using a folding rule and length of branches and trunk circumference was measured with a measuring tape. Diameter of branches has been measured using a sliding caliper. Wood surface area has been calculated using circumference and height data of the trees and calculating truncated cone or cone (for top segment) surface area (without the top and bottom) for each of the measured segments and adding calculated surface area of the branches. Branches surface area was calculated using the length of the branch and largest diameter with the cone surface formula (without bottom).

6.1.3 Soil moisture measurements

Soil water content was determined using two different measurement systems (TDR and FDR). Additionally, tensiometers have been installed to measure soil water tension. All soil moisture related measurements were only conducted in 'Wellant' treatments. Two tensiometers (M-Tensiometer, Tensio-Technik, Geisenheim, Germany) per depth were installed at 25 and 50 cm depth in each of the three treatments CT, NT, and ET. Tensiometers are able to measure soil moisture tension in a range between 0 and about -850 hPa. Tensiometer measurements were conducted between DOY 103 and DOY 323 in 2012, and between DOY 95 and DOY 301 in 2013.

Additionally, a TDR100 system with CS605 probes (Time domain reflectometry; Campbell Scientific, Inc., Logan, UT, USA) has been used. TDR probes were installed at 30, 60 and 90 cm depth, but all sensors at 90 cm failed soon after installation. One TDR probe per depth, per treatment has been installed. TDR probes in 30 cm depth recorded data continuously starting from day of year (DOY) 133 in 2012 until DOY 301 in 2013.

16 Diviner 2000 (FDR, frequency domain reflectometry; Sentek Pty Ltd, Stepney, SA, Australia) access tubes were installed in the field. Diviner 2000 measurements were conducted weekly during the growing season and once to twice per month during the rest of the year. Additional Diviner 2000 measurements were conducted after abundant rain falls. The Diviner 2000 takes measurements every 10 cm, down to the maximum depth (e.g. in 10 cm, 20 cm, 30 cm, ..., 160 cm depth).

6.1.4 Leaf area and light interception

Light interception (LI) was recorded by using 20 PAR sensors (TRANSFLO NZ LTD, Palmerston North, New Zealand) mounted on 4 planks (5 sensors per plank, 25 cm distance between planks) and one reference PAR sensor besides the orchard. Positions of LI measurements have been changed two times per treatment in 2012 and 2013. All LI measurements were conducted after shoot cessation in both years. LI has been recorded for several days with high radiation. Interception of 20 PAR sensors between trees was compared to reference sensor PAR interception and average % of LI for one day was calculated. Additionally tree height, number of spurs and long shoots, total length of long shoots and number of fruits has been measured for trees surrounding the LI measurement planks.

Leaf area of 20 long shoots and 20 spurs per treatment and cultivar has been measured in 2013 using a LI-3100C Area Meter (Li-COR Inc., Lincoln, NE, USA). Length of shoot, number of leaves per shoot, and, for every single leaf, leaf area has been measured. Fresh weight and dry weight (dried for 48 h at 75 °C) for all leaves of one shoot has been quantified. Total leaf area of trees used for LI measurements has been calculated by using a relationship found between leaf area and shoot length (shown in the results) for long shoots with measured shoot lengths, and multiplying spur numbers with average spur leaf area of the particular cultivar.

6.1.5 Tree water potential measurements

For all predawn and midday stem water potential measurements fully expanded, healthy looking leaves were excised and water potential was immediately measured in the field using a pressure chamber (SCHOLANDER et al., 1965) of type PMS 600 (PMS Instruments, Albany, Oregon, USA). Predawn water potential measurements (Ψ_{pd}) were conducted early in the morning and finished before dawn, at least 1 hour prior to sunrise. For midday stem water potential measurements (Ψ_{stem}), shaded leaves, which were situated in the lower part of the tree close to the trunk, have been placed in aluminum foiled bags for 2 hours prior to measurements. Ψ_{stem} measurements were performed around solar noon (+/- 1 hour).

Water potential was measured using one leaf per tree, on three trees per treatment. For 'Wellant' at least one measurement per week was performed during the growing season. Water potential and leaf gas exchange measurements were usually performed on the same trees per treatment and on the same day. In case, this was not possible, measurements were performed on the same trees on two consecutive days.

6.1.6 Gas exchange measurements

For leaf gas exchange measurements a LI-6400XT portable photosynthesis system with a 6400-02B LED light source has been used (Li-COR, Lincoln, NE, USA). All single point gas exchange measurements were conducted with the following settings: CO_2: 380 µmol mol^{-1}; flow: 300 µmol s^{-1}; light intensity: 1750 µmol m^{-2} s^{-1}; relative humidity: 38 - 50 %; temperature: 25 ± 5 °C. This type of measurement at the fixed saturating light intensity of 1750 µmol m^{-2} s^{-1} is called PN1750 in the following. PN1750 measurements were logged every 10 seconds for three minutes after all settings were set and gas exchange rates were stable. They were performed between 9:00 a.m. and 4:30 p.m., and time of measurement has also been logged. Net photosynthetic rate (Pn; in µmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s; in mol H_2O m^{-2} s^{-1}), intercellular CO_2 concentration (C_i; µmol CO_2 mol^{-1}), and transpiration (E; in mmol H_2O m^{-2} s^{-1}) data were already calculated by the LI-6400 system.

On DOY 221 in 2012, and on DOY 157 in 2013, whole day PN1750 measurements, during the light period from dawn until dusk, have been conducted. For these short time photosynthesis measurements, the same settings were used as described above, instead of using outside light conditions, to achieve stable and comparable values between treatments. Measurements per leaf were logged every ten seconds for three minutes. Three leaves per treatment were marked and always the same three leaves were measured repeatedly during the whole day.

Light response curve (LRC) measurements were conducted with the same settings as PN1750 measurements except for light intensity. A minimum waiting time of 120 seconds and a maximum waiting time of 240 seconds per light setting were used. Light settings applied were 2000, 2000, 2000, 2000, 2000, 1750, 1500, 1000, 700, 500, 300, 100, 50, 0, 0, 0 µmol m^{-2} s^{-1}. For statistical analysis light response curves were fitted according to equation 6 of LOBO et al. (2013).

6.1.7 Harvest

In 2012, all fruitlets were removed immediately after bloom to allow all trees a good development during their first growing season after planting. First harvest of trees was conducted in 2013. Harvest date has been determined using the Streif-Index (STREIF, 1989) (firmness divided by soluble solids content and starch degradation class) of boundary trees. During harvest, total yield per tree and fruit number per tree has been measured for all trees in the field except for boundary trees. Fruits of 12 trees per treatment were sorted according to diameter classes. 52 healthy and ordinary looking fruits per treatment were taken to a laboratory for further measurements. In the laboratory fresh weight (g), soluble solids content (% Brix), flesh firmness (kg cm^{-2}), and starch degradation (class 1 to 10) has been determined for every single fruit. Malic acid (g L^{-1}) was measured by taking together juice of 3 fruits.

6.1.8 Statistics

Data of the experiments were statistically analyzed by using SPSS 21.0 (IBM SPSS Statistics, 2012). All data has been tested for normal distribution and homogeneity of variance. Analysis of Variance (ANOVA) has been used to explore statistically significant differences between treatments (in the following referred to as ‘significant’). In case, the test for normal distribution was negative, the Kruskal-Wallis test was used to test for differences. Tukey’s HSD test has been used as a post-hoc test for more than two groups and when homogeneity of variance was positive. Otherwise the Games-Howell post-hoc test was chosen. All tests were performed at a significance level of $p \leq 0.05$. Groups with a different letter in the results section are significantly different at $p \leq 0.05$.

6.2 Results

6.2.1 Phenological observations and tree descriptions

Bud break in 2012 has been observed for all three cultivars on DOY 80. Full bloom was recorded on DOY 122 for 'Sapora', on DOY 125 for 'Wellant', and for 'Jugala' on DOY 128. In 2013, bud break of 'Sapora' was observed on DOY 89, and on DOY 90 for 'Jugala' and 'Wellant'. Full bloom occurred on DOY 126 for 'Sapora' and 'Wellant', and on DOY 128 for 'Jugala'.

Overall in 2012, except for number of long shoots in 'Jugala' and number of spurs in 'Wellant', a significant difference was found for CT compared to NT trees (Table 7). Interestingly for 'Jugala' and 'Sapora', CT had the lowest total length of new long shoots and the smallest wood surface area, but the highest numbers of spurs and flowers, compared to NT and ET. 'Wellant' showed a similar result for total length of new shoots and wood surface area, but number of flowers for CT was lower than for NT. Although total length of new long shoots of 'Jugala' in 2012 was significantly lower in CT compared to NT and ET, no significant difference in number of long shoots per tree was found between treatments. For 'Sapora' and 'Wellant', CT had significantly lower numbers of new long shoots and a shorter total length of new long shoots compared to NT and ET.

Table 7: Tree counting and measurements in 2012 for 'Jugala', ' Sapora', and 'Wellant', including number of new long shoots (LS) on DOY 282, total length of new long shoots (LLS; in cm) on DOY 282, number of spurs (SS) on DOY 128, number of flowers (FL) on DOY 123, and calculated wood surface area (WSA; in m^2) on DOY 285. Data is presented for CT, NT, ET, and additionally total average (Total) is shown. Mean values (n=12) followed by a different letter in each column are significantly different at $p \leq 0.05$.

Jugala	**LS**	**LLS**	**SS**	**FL**	**WSA**
CT	17.4 ± 3.53 a	140.6 ± 64.63 a	45.1 ± 8.14 a	101.5 ± 33.94 a	0.11 ± 0.02 a
NT	18.7 ± 4.12 a	368.2 ± 80.83 b	28.7 ± 12.73 b	61.2 ± 45.00 b	0.18 ± 0.02 b
ET	19.6 ± 2.47 a	353.7 ± 132.07 b	28.9 ± 8.97 b	87.6 ± 33.55 ab	0.17 ± 0.04 b
Total	18.6 ± 3.46	287.5 ± 141.35	34.2 ± 12.56	83.4 ± 40.50	0.15 ± 0.04
Sapora	**LS**	**LLS**	**SS**	**FL**	**WSA**
CT	10.5 ± 2.58 a	84.4 ± 23.81 a	38.1 ± 7.80 a	124.4 ± 23.68 a	0.10 ± 0.01 a
NT	14.3 ± 3.79 b	247.2 ± 49.90 b	28.8 ± 6.44 b	97.5 ± 39.10 ab	0.15 ± 0.02 b
ET	14.3 ± 2.96 b	217.0 ± 76.19 b	30.1 ± 9.00 b	91.9 ± 31.78 b	0.15 ± 0.03 b
Total	13.0 ± 3.55	182.9 ± 89.02	32.3 ± 8.65	104.6 ± 34.37	0.13 ± 0.03
Wellant	**LS**	**LLS**	**SS**	**FL**	**WSA**
CT	13.3 ± 1.91 a	101.3 ± 30.91 a	34.6 ± 7.12 ab	141.2 ± 41.20 a	0.11 ± 0.01 a
NT	21.7 ± 3.08 b	273.4 ± 78.93 b	39.2 ± 6.93 a	190.4 ± 26.58 b	0.17 ± 0.03 b
ET	20.6 ± 2.64 b	317.5 ± 69.12 b	31.2 ± 6.45 b	166.2 ± 41.24 ab	0.18 ± 0.02 b
Total	18.5 ± 4.55	230.7 ± 112.76	35.0 ± 7.42	165.9 ± 41.30	0.15 ± 0.04

In 2013, the cultivars showed an inconsistent result (Table 8). For 'Wellant', CT had significantly lower values in all measured parameters than NT. Number of new long shoots did not differ between treatments in 'Sapora', while for 'Jugala' only between CT and ET differences were found. For 'Wellant', NT had significantly higher numbers of new long shoots than CT and ET. Total length of new long shoots was lowest for CT in 'Jugala' and 'Wellant', but for 'Sapora' no statistically significant difference between treatments was found. Number of spurs of 'Wellant' was significantly lower in CT than in NT and ET. For 'Sapora' the number of spurs was significantly higher in NT, than in ET and CT. For 'Jugala', only the two irrigated treatments NT and ET had statistically significant different numbers of spurs in 2013. Number of flowers per tree was highest in NT for all three cultivars in 2013. For all investigated cultivars in 2013, wood surface area was lowest in CT, while NT showed the highest wood surface area.

Table 8: Tree counting and measurements in 2013 for 'Jugala', ' Sapora', and 'Wellant', including number of new long shoots (LS) on DOY 147, total length of new long shoots (LLS; in cm) on DOY 214, number of spurs (SS) on DOY 147, number of flowers (FL) on DOY 100, and calculated wood surface area (WSA; in m^2) on DOY 213. Data is presented for CT, NT, ET, and additionally total average (Total) is shown. Mean values (n=12) followed by a different letter in each column are significantly different at $p \leq 0.05$.

Jugala	**LS**	**LLS**	**SS**	**FL**	**WSA**
CT	27.0 ± 4.55 a	573.8 ± 168.28 a	73.8 ± 19.06 ab	241.7 ± 42.66 a	0.19 ± 0.04 a
NT	23.3 ± 4.31 ab	758.3 ± 126.69 b	92.7 ± 24.55 a	374.6 ± 69.30 b	0.26 ± 0.03 b
ET	20.9 ± 4.70 b	692.6 ± 155.03 ab	70.2 ± 15.31 b	290.0 ± 75.17 a	0.24 ± 0.04 b
Total	23.8 ± 5.07	674.9 ± 165.82	78.9 ± 21.85	302.1 ± 83.43	0.23 ± 0.04
Sapora	**LS**	**LLS**	**SS**	**FL**	**WSA**
CT	20.8 ± 3.71 a	629.6 ± 89.54 a	47.3 ± 7.58 a	179.2 ± 34.76 b	0.21 ± 0.02 a
NT	21.7 ± 5.43 a	712.3 ± 140.69 a	70.3 ± 18.28 b	400.8 ± 132.04 a	0.25 ± 0.03 b
ET	22.3 ± 5.50 a	676.7 ± 91.43 a	55.6 ± 13.89 a	212.9 ± 56.63 b	0.24 ± 0.02 b
Total	21.6 ± 4.84	671.6 ± 111.37	57.8 ± 16.64	264.3 ± 129.03	0.23 ± 0.03
Wellant	**LS**	**LLS**	**SS**	**FL**	**WSA**
CT	22.9 ± 3.26 a	587.8 ± 146.76 a	44.3 ± 7.89 a	133.8 ± 37.42 a	0.20 ± 0.03 a
NT	40.2 ± 7.84 b	1120.1 ± 306.72 b	76.0 ± 11.79 b	312.9 ± 72.19 c	0.34 ± 0.07 c
ET	29.2 ± 7.47 a	906.6 ± 212.94 b	62.8 ± 22.82 b	235.0 ± 66.02 b	0.28 ± 0.07 b
Total	30.8 ± 9.62	863.1 ± 315.67	61.0 ± 20.03	227.2 ± 94.77	0.27 ± 0.08

Shoot growth stopped in 2012 for 'Jugala' on DOY 186 in CT, on DOY 212 in ET, and on DOY 205 for NT; for 'Wellant' on DOY 179 in CT, and on DOY 186 in ET and NT; and for 'Sapora' on DOY 186 in CT and ET, and on DOY 193 in NT. In 2013, end of shoot growth of 'Sapora' and 'Jugala' did not differ between treatments (recorded on DOY 178). For 'Wellant' shoot growth stopped on DOY 178 in CT, and on DOY 192 in ET and NT.

6.2.2 Soil moisture measurements

6.2.2.1 Tensiometers

Soil moisture tension started off on DOY 103 with similar values (Figure 7 A), but during the season ET showed a different course in 25 cm depth compared to CT and NT. For ET, all irrigation and higher precipitation events clearly correspond to increases of soil moisture tension. CT tensiometer values varied between -440 hPa and -148 hPa from DOY 103 until DOY 180. After this day CT values decreased stepwise and showed very low values until DOY 290. Increases of CT values in 25 cm depth correspond with precipitation (Figure 7 D). NT showed a first low value around DOY 122 of -631 hPa, which did not correspond to irrigation and also is lower than the values of CT, but then increased again for the period between DOY 137 and DOY 174 with values higher than -200 hPa. After this point values of NT decreased stepwise down to -865 hPa. Except for the values from the beginning of the season until DOY 135 increases in tensiometer values in NT correspond to irrigation events and to higher rainfall events in 25 cm depth. Interestingly, NT shows a more similar course to CT than to ET in 25 cm depth, while in 50 cm depth (Figure 7 B) NT and ET display a more similar course than compared to CT. The soil moisture tension of CT in 50 cm depth is continuously decreasing through the season, with precipitation events leading mainly to a less steep decrease or to stable values for a few days. In 50 cm depth tensiometer values of NT and ET stayed above -367 hPa during the whole irrigation period and irrigation events are clearly visible (Figure 7 C) with a slight delay compared to values in 25cm depth.

In 2013 the courses of soil moisture tension in 25 cm depth (Figure 8 A) of the three treatments are interwoven compared to 2012. Between DOY 200 and 255 CT showed the lowest values compared to ET and NT, with values at the lowermost measurement range of the tensiometers. The course of ET showed a high variability during the season, changing between values of under -700 hPa and -60 hPa. NT displayed an in between CT and ET behavior, with lower fluctuations than ET. Soil moisture tension of CT in 50 cm depth showed the lowest values throughout most of 2013 (Figure 8 B). Seasonal courses of CT mainly match between 25 and 50 cm depth and changes partly correspond to previous rain events (Figure 8 D). ET and NT stayed above -605 hPa until DOY 265 for ET and DOY 268 for NT. In ET and NT, irrigation events are clearly visible in 25 and 50 cm depth. Overall, tensiometer and TDR measurements (see Appendix) indicate similar results and confirm each other in the general course of the treatments. Both measurements show highest moisture in ET during most of both seasons and in all depths, while for CT mainly the lowest values were recorded.

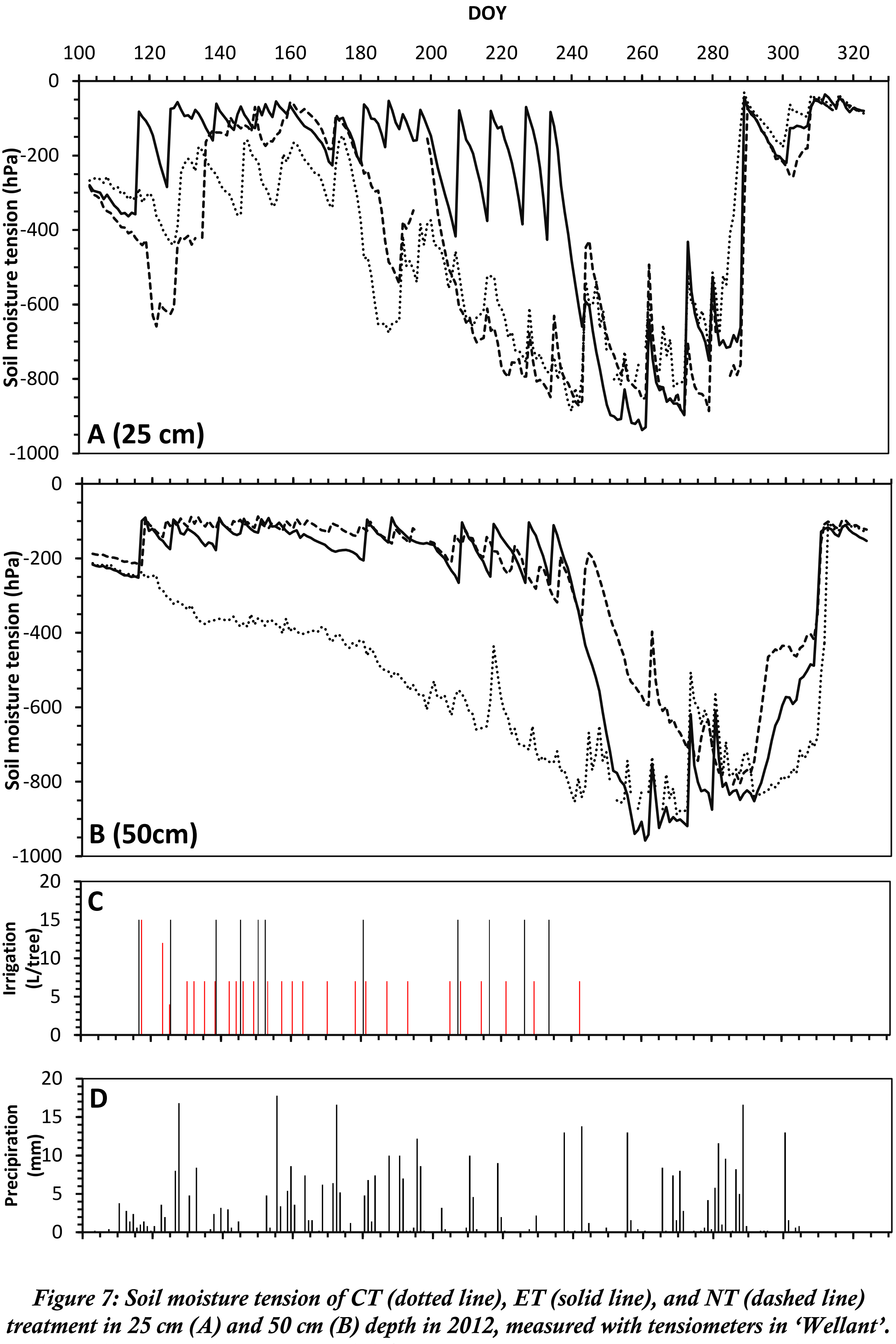

Figure 7: Soil moisture tension of CT (dotted line), ET (solid line), and NT (dashed line) treatment in 25 cm (A) and 50 cm (B) depth in 2012, measured with tensiometers in 'Wellant'. Additionally, recorded precipitation (D) from DOY 103 to DOY 305 and irrigation (C) applied in 2012 (from bloom to end of August to prevent regrowth of terminated shoots) for NT (red) and ET (black) is displayed.

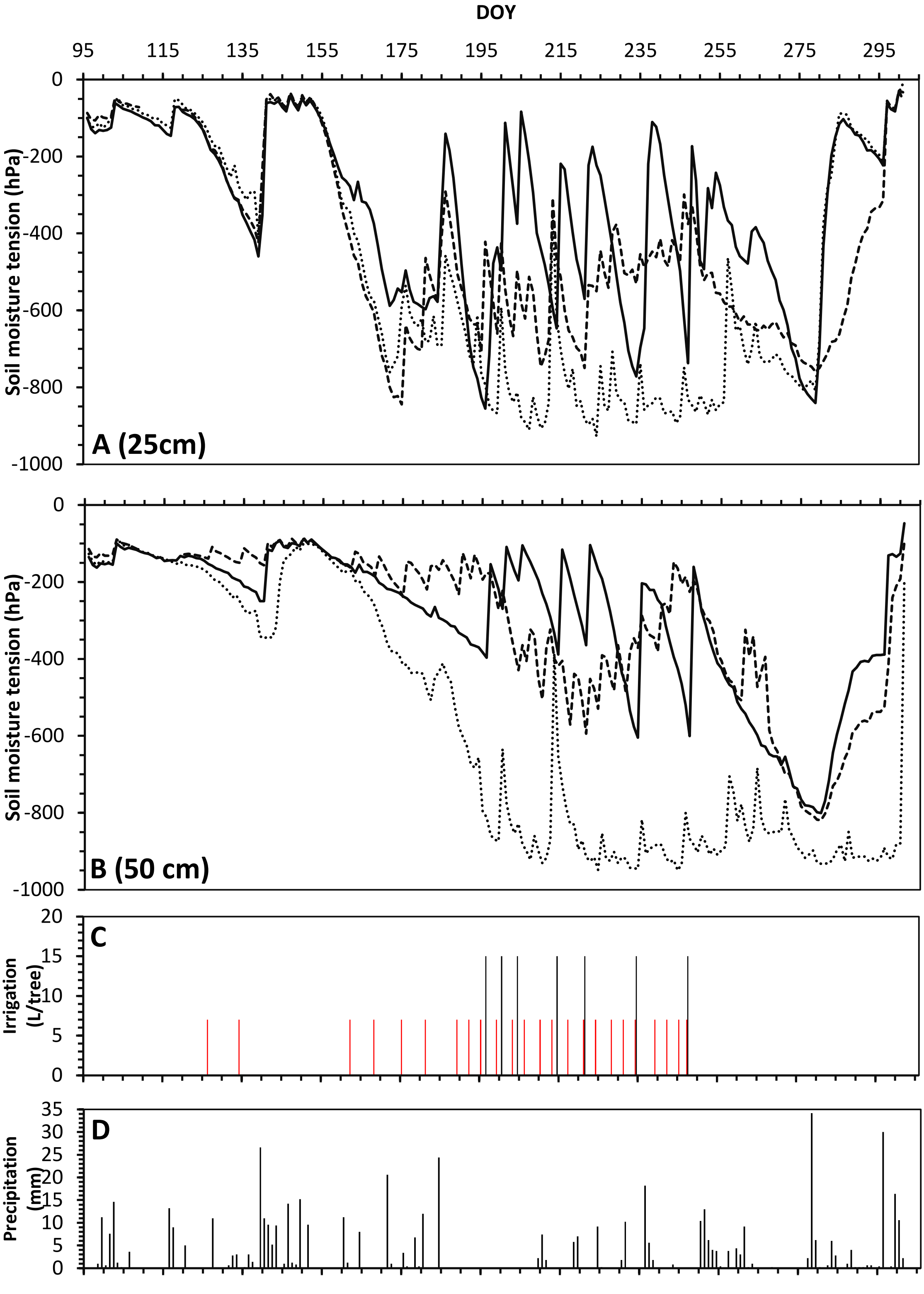

Figure 8: Soil moisture tension of CT (dotted line), ET (solid line), and NT (dashed line) treatment in 25 cm (A) and 50 cm (B) depth in 2013, measured with tensiometers in 'Wellant'. Additionally, recorded precipitation (D) from DOY 96 to DOY 301 and irrigation (C) applied in 2013 (from bloom to beginning of September (to prevent regrowth of terminated shoots)) for NT (red) and ET (black) is presented.

6.2.2.2 Diviner 2000 measurements (soil water content)

SWC measurements from 10 cm to 80 cm soil depth show in general a similar behavior, while from 90 to 160 cm depth no relevant changes during the measurement period from 2012 to 2013 have been visible (see Figure 9 and Appendix). SWC of NT was highest, in most depths during most of 2012 and 2013, while CT was lowest and ET in between both.

In 2012, NT and ET showed clearly higher SWC in 20 and 30 cm depth compared to CT during the irrigation period. SWC of CT continually decreased in these soil layers until mid-October 2012. In 2013 growing season, SWC of ET in 20 and 30 cm depth was clearly higher than in CT. A decrease of SWC in NT and ET is visible in both years after irrigation was stopped. Interestingly, SWC of CT below 50 cm depth did not vary much until July 2013, where a clear drop of SWC was visible in 50 to 80 cm depth. For NT, SWC noticeably decreased already during August 2012 in 50 to 80 cm depth, while at the same time for ET a clear decrease was only visible in 50 cm depth. In 2013, no clear changes occurred for NT and ET below 40 cm depth.

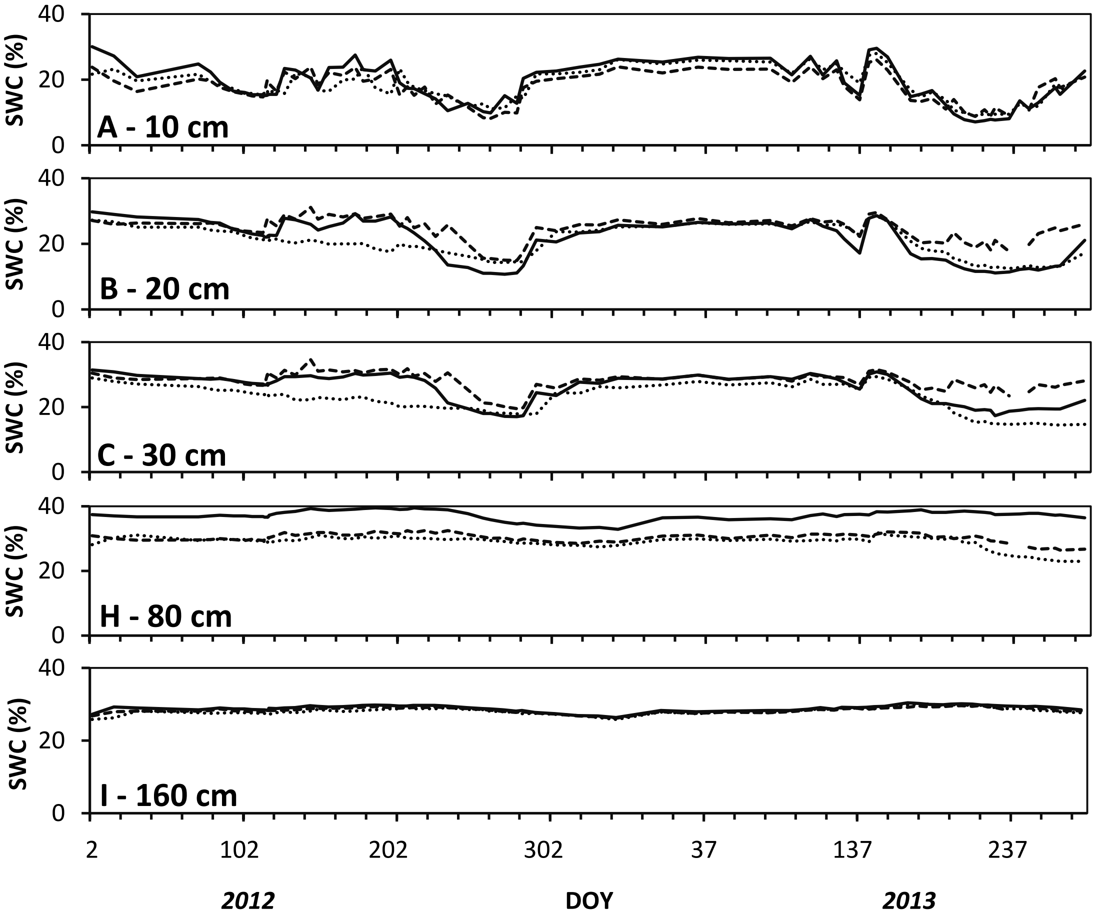

Figure 9: Diviner 2000 soil water content (SWC) measurements in 10 cm (A), 20 cm (B), 30 cm (C), 80 cm (H), and 160 cm (I) depth for CT (dotted line), ET (dashed line) and NT(solid line), 2012-2013.

6.2.3 Light interception (LI)

Measured LI of CT trees was significantly lower in 2012 and 2013 compared to NT and ET (Table 9). While trees of CT intercepted an average of 17.4 % of available PAR in 2012, NT and ET trees intercepted 24.2 % and 26.3 %, respectively. In 2013, PAR interception was 24.9 % for CT, 38.3 % for NT and 42.1 % for ET.

Table 9: Mean intercepted PAR in % for 'Wellant' in 2012 and 2013 for CT, NT, and ET. Mean values (n=34) and standard deviations followed by a different letter in each column are significantly different at p ≤ 0.05.

	% PAR Intercepted 2012	% PAR Intercepted 2013
CT	17.4 ± 4.7 a	24.9 ± 7.7 a
ET	26.3 ± 6.1 b	42.1 ± 14.2 b
NT	24.2 ± 5.6 b	38.3 ± 6.0 b

Measurements on trees that were used for the LI measurements did not show statistically significant differences between treatments for total length of long shoots, tree height and numbers of fruits (Table 10). But on a 10 % significance level, long shoot length of CT was significantly lower than the one of NT and ET. Number of spurs in NT was significantly higher than in CT, while ET was in between. Treatment CT showed the lowest number of spurs with an average of only 36.

Table 10: Measurements of total length of long shoots (TLLS) in cm, tree height (Height) in cm, number of spurs (# Spurs) and number of fruits (# fruits) of trees where LI was measured in 2013. Average values (n=6) and standard deviations followed by a different letter in each column are significantly different at p ≤ 0.05.

	TLLS (cm)	Height (cm)	# Spurs	# Fruits
CT	507.5 ± 160.3 a	223.3 ± 11.2 a	36.0 ± 7.2 a	29.3 ± 6.0 a
ET	847.2 ± 77.2 a	231.7 ± 14.8 a	50.3 ± 4.0 ab	20.3 ± 9.2 a
NT	899.5 ± 265.5 a	225.3 ± 16.0 a	66.3 ± 5.5 b	35.3 ± 22.2 a

Additionally, leaf area (LA) measurements were conducted for 'Wellant' trees. No statistically significant differences were found between treatments for spur LA. Average LA of spurs was 81.8 cm^2. LA of long shoots was not significantly different between treatments for shoots of the same length. A relationship between LA and length of long shoots (> 5 cm) has been found (see Appendix). This relationship and the average measured LA of spurs have therefore been used for total LA calculation (Table 11) of trees, where LI was measured (Table 10). Leaf numbers for total LA calculation were counted on the same trees. Calculated total LA was significantly lower in CT trees compared to NT and ET trees (Table 11). Between NT and ET trees, no statistically significant difference has been found in calculated total leaf area.

Table 11: Calculated total leaf area (Calc LA) for CT, ET, and NT of 'Wellant' trees (2013), where LI was measured. Average values (n=6) and standard deviations followed by a different letter in each column are significantly different at $p \leq 0.05$.

	Calc LA (m^2)
CT	1.07 ± 0.22 a
ET	1.72 ± 0.14 b
NT	1.89 ± 0.36 b

By using the calculated total leaf area, LAI (leaf area index) has been calculated. LAI for CT was 0.33, for ET was 0.54, and for NT was 0.59 in 2013.

6.2.4 Tree water potential measurements

In 2012, CT showed the lowest predawn water potential (Ψ_{pd}) values of the three treatments on every measurement day (Figure 10). Lowest average Ψ_{pd} value of CT was -0.56 MPa, of ET was -0.34 MPa, and of NT was -0.43 MPa. All lowest values were measured on DOY 255 when additional irrigation has been stopped already in all treatments (ET on DOY 233; NT on DOY 242). Except for this day, NT and ET never showed values below -0.25 MPa. For CT, Ψ_{pd} values were found to be below -0.25 MPa on DOY 171 and on all measurements conducted after DOY 221.

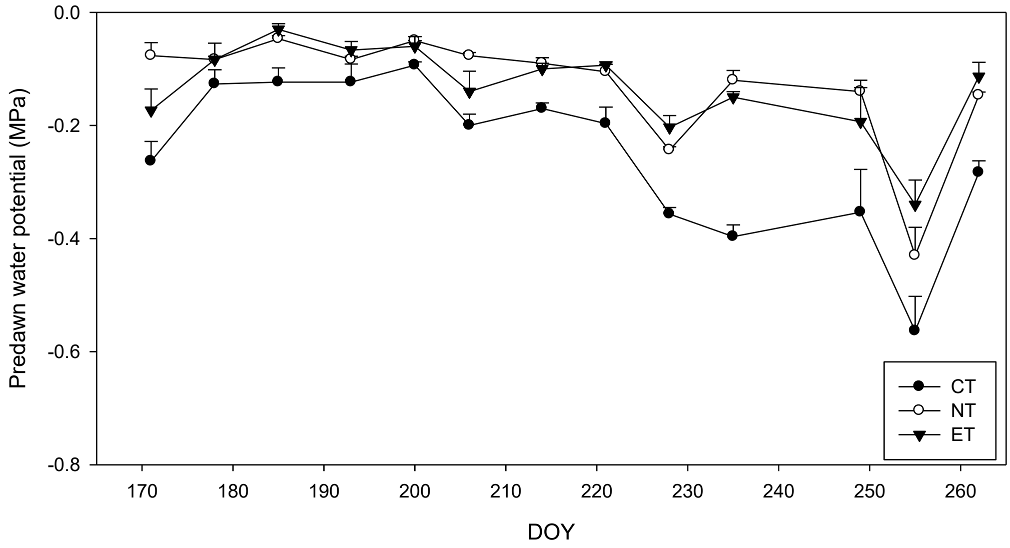

Figure 10: Average predawn leaf water potential (n=3) for 'Wellant' CT, NT, and ET in 2012, bars indicate standard deviations. For exact values and statistic results see Appendix Table 22.

CT was significantly different from NT for all measurement dates except for DOY 178 and DOY 193. ET differed significantly from CT on 10 out of the 13 measurement dates (see Appendix Table 22). The two irrigated treatments NT and ET had significantly different values on DOY 171, 206, and 228. Total seasonal average of Ψ_{pd} during 2012 was -0.25 ± 0.14 MPa for CT, -0.13 ± 0.10 MPa for NT, and -0.13 ± 0.08 MPa for ET. In general, treatments had high values until about DOY 220. After this day Ψ_{pd} became more negative in all three treatments until DOY 262. This generally corresponds to soil moisture measurements. Major visible drops on DOY 228 and 255 correspond to low soil moisture contents in combination with high night temperatures of 15.7 °C and 14 °C, respectively.

In 2013, Ψ_{pd} was not statistically significantly different between all three treatments until DOY 197. After this point, CT showed the lowest values compared to NT and ET except for DOY 240 and 260. On these two days values of all three treatments showed similar values. Lowest Ψ_{pd} in 2013 was -0.45 MPa for CT on DOY 217, -0.25 MPa for NT on DOY 234, and -0.19 MPa for ET on DOY 247. On DOY 197, Ψ_{pd} of CT was significantly lower than of NT, while ET was in between. On DOY 213 and 217 Ψ_{pd} of CT was significantly different from ET and NT, while it was significantly different from ET but not from NT on DOY 234. In 2013, overall mean Ψ_{pd} value of CT was -0.17 ± 0.12 MPa, of NT was -0.12 ± 0.05 MPa, and of ET was -0.11 ± 0.05 MPa.

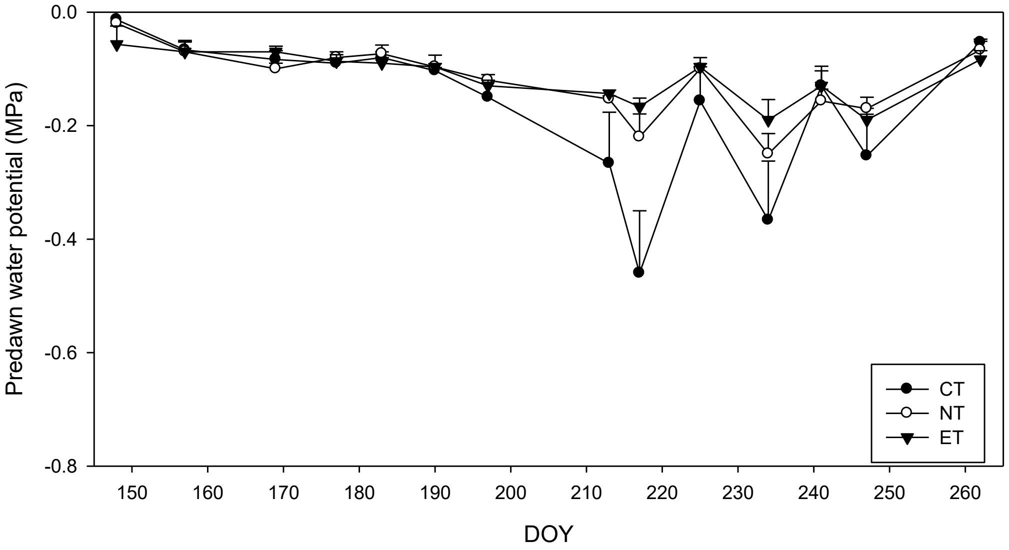

Figure 11: Average predawn leaf water potential (n=3) of CT, NT, and ET for 'Wellant' in 2013, error bars indicate standard deviations.

In general, Ψ_{pd} values did not differ much between treatments in 2013. Only late in the season, between DOY 210 and 250, minor differences were visible. This shows that 2013 was a wetter year than 2012 and also corresponds with TDR and tensiometer results. Overall, mean Ψ_{pd} value of CT was lower in 2012 than in 2013, while overall values of NT and ET were similar between years.

Midday stem water potential (Ψ_{stem}) of 'Wellant' in 2012 (Figure 12) showed a higher variability compared to Ψ_{pd}. Except for the first measurement day, Ψ_{stem} of CT showed the lowest values throughout the whole season 2012. On DOY 166, measured soil moisture content and tension were very similar between treatments (see Appendix Figure 28 on page 134; see Figure 7 on page 58).

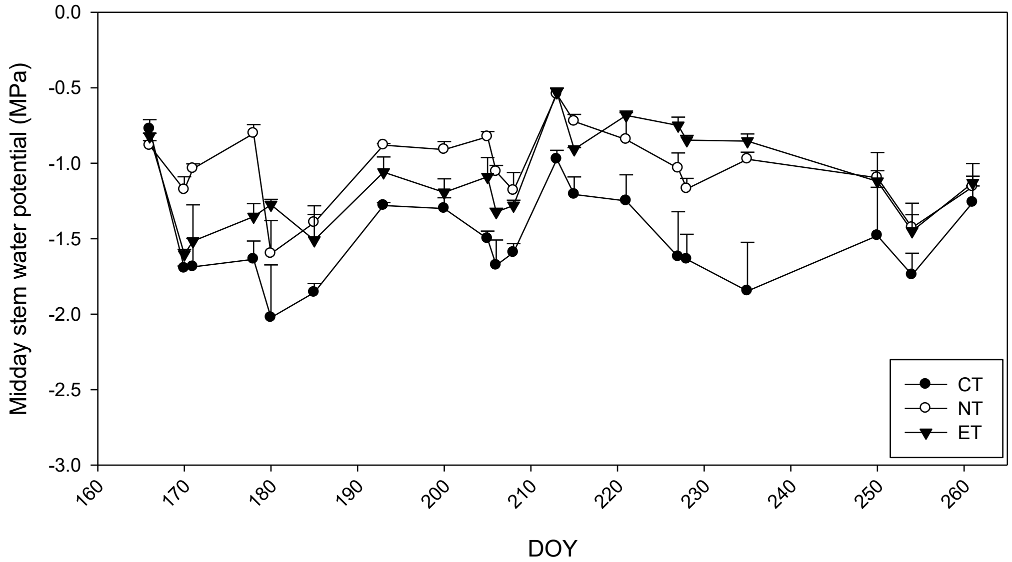

Figure 12: Average midday stem water potential (n=3) of CT, NT, and ET of 'Wellant' in 2012, error bars indicate standard deviations.

Ψ_{stem} of CT was significantly different from Ψ_{stem} of NT on 16, and significantly different from Ψ_{stem} of ET on 12 out of 20 measurement days (see Appendix Table 23). No statistically significant differences between all three treatments were found on DOY 180, due to a high variability, and after DOY 250, where treatments have not been irrigated anymore and measured soil moisture tension was low in all treatments. Clearly visible drops in all three treatments correspond to days with high maximum VPD values of 3 kPa and higher (e.g. 4.8 kPa on DOY 208, and 3.6 kPa on DOY 254). Ψ_{stem} of ET and NT were above -1,5 MPa during most of the season 2012. Seasonal mean values in 2012 were -1.5 ± 0.34 MPa for CT, -1.1 ± 0.31 MPa for ET, and -1.0 ± 0.26 MPa for NT.

In 2013, Ψ_{stem} values were very similar for all three treatments (Figure 13). Only on DOY 169 and 217, statistically significant differences were found. On DOY 169 Ψ_{stem} of CT was significantly different from Ψ_{stem} of NT and ET, which corresponds to much lower tensiometer values. In addition, a very high VPD of 4.1 kPa has been measured on this day. On DOY 217, the two irrigated treatments NT and ET showed statistically significant differences between each other, but not to CT, although soil moisture tension of CT was much lower than in NT and ET. NT has been irrigated on DOY 217 and a very high VPD of 4.0 kPa has been measured. The major visible peak on DOY 177 corresponds to a low VPD of 1.2 kPa and similar soil moisture contents. Mean seasonal value of Ψ_{stem} (2013), was -1.32 ± 0.34 MPa for CT, -1.22 ± 0.3 MPa for NT, and -1.26 ± 0.31 MPa for ET.

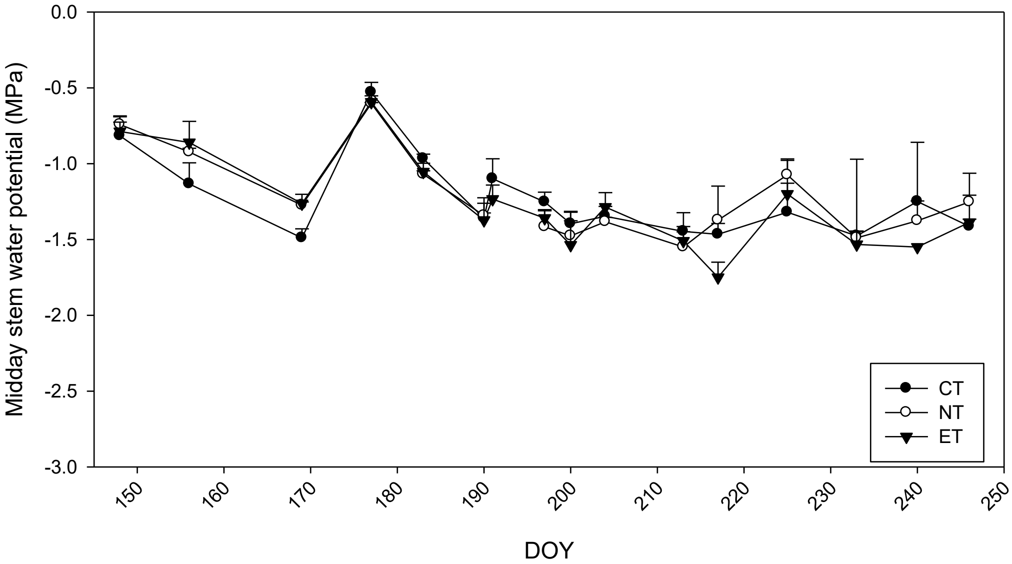

Figure 13: Average midday stem water potential (n=3) of CT, NT, and ET for 'Wellant' in 2013, error bars indicate standard deviations.

6.2.5 Gas exchange measurements

Similar to Ψ_{pd} and Ψ_{stem}, net photosynthetic rate (PN1750; at a light intensity of 1750 μmol m^{-2} s^{-1}) of CT showed the lowest values during most of season 2012, starting from DOY 180 (Figure 14). Major drops of values for all treatments can be seen on DOY 180, 206 and 254. These days had a high maximum day temperature of 32 °C and higher maximum VPD levels compared to other measurement days, of 3.1, 3.2, and 3.6 kPa, respectively. Lowest mean value of CT was 5.5 μmol m^{-2} s^{-1}, and of NT and ET was 7.8 and 7 μmol m^{-2} s^{-1}, on DOY 180 (see Appendix Table 24). Highest average PN1750 for CT was recorded on DOY 170, with 18.4 μmol m^{-2} s^{-1}. For NT, highest mean PN1750 was 19.1 μmol m^{2} s^{-1}, on DOY 193, while ET showed a highest average PN1750 of 16.1 μmol m^{-2} s^{-1} on DOY 170.

Photosynthetic rate of NT has been significantly higher than of CT on DOY 171, 178, between DOY 193 and 221, and on DOY 250 (see Appendix Table 24). Except for DOY 178 and 250, this corresponds to Ψ_{stem} results. For DOY 250 no statistically significant difference has been found for Ψ_{stem}, but average value of CT was -1.5 MPa, while NT had an average value of -1.1 MPa. On DOY 178, CT surprisingly shows a significantly higher

PN1750 rate than NT, although Ψ_{stem} of CT was lower with -1.6 MPa than Ψ_{stem} of NT with -0.8 MPa. Apart from this exception, NT rates were higher than CT rates during the rest of the season in 2012. The greatest difference between CT and NT on the same day was measured on DOY 208, with an average photosynthetic rate of 6 µmol m^{-2} s^{-1} in CT, and of 12 µmol m^{-2} s^{-1} in NT.

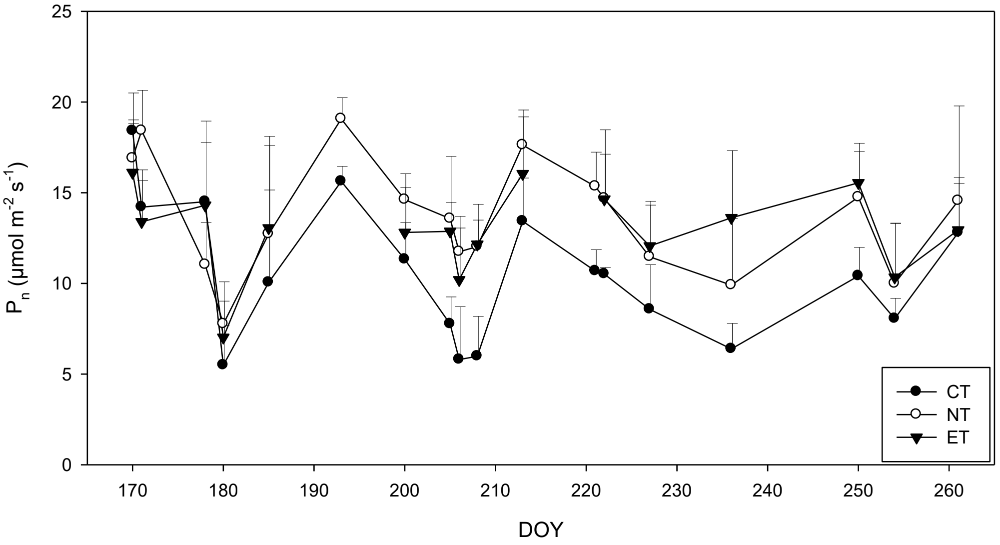

Figure 14: Average leaf photosynthetic rate at saturating light intensity (PN1750) in 2012 for CT, NT, and ET of 'Wellant' (9 a.m. to 4.30 p.m.), error bars indicate standard deviations (n=3-12, depending on weather conditions on the specific measurement day; n is similar for all treatments for one specific measurement day and measurements were performed at a similar time of day).

In 2013, measured photosynthetic rates were very similar and no statistically significant difference between treatments was found until DOY 212 (Figure 15). On DOY 212, 218, and 241, CT values were statistically significantly lower than PN1750 values of ET, while NT was intermediate. This corresponds to soil moisture tension in 25 and 50 cm depth.

Highest mean value of CT with 17.9 ± 2.48 µmol m^{-2} s^{-1} occurred on DOY 177. On DOY 182 highest mean value of 20.4 ± 1.44 µmol m^{-2} s^{-1} for ET has been measured. NT showed the highest mean value of 18.2 ± 1.41 µmol m^{-2} s^{-1} on DOY 234. Lowest average photosynthetic rates in 2013 were 8.4 ± 5.22 µmol m^{-2} s^{-1} on DOY 218 for CT, 13.2 ± 0.63 µmol m^{-2} s^{-1} on DOY 200 for ET, and 12.4 ± 2.12 µmol m^{-2} s^{-1} on DOY 198 for NT.

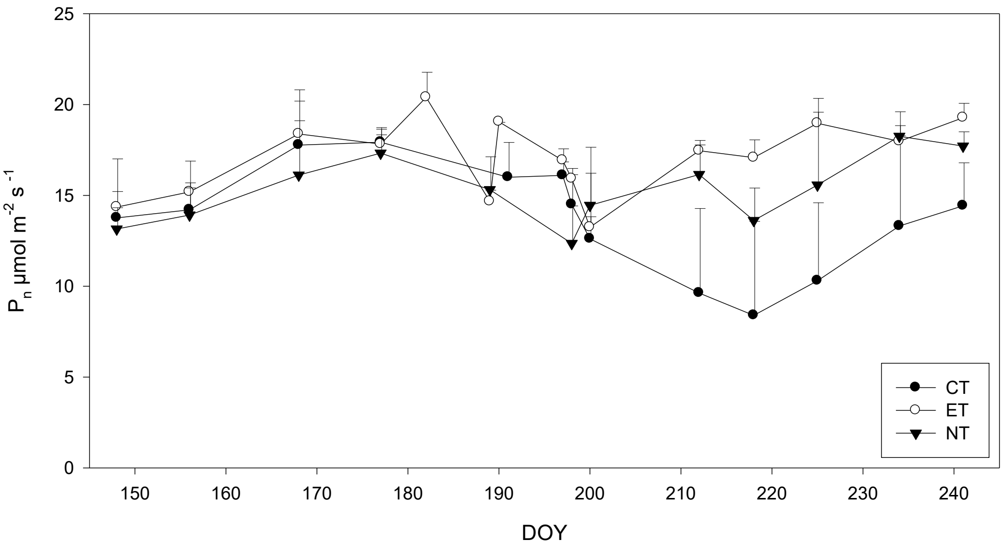

Figure 15: Seasonal course of leaf photosynthetic rate at light saturation (PN1750) in 2013 for CT, NT, and ET, error bars indicate standard deviations (n=3-9, depending on weather conditions on the specific measurement day; n is similar for all treatments for one specific measurement day and measurements were performed at a similar time of day).

On the 8th of August 2012 (DOY 221) a full day PN1750 measurement has been conducted for treatments NT and CT (see Appendix Figure 34). Predawn water potential of CT was -0.2 MPa and statistically significantly lower as Ψ_{pd} of NT (-0.11 MPa). The same was found for Ψ_{stem}, with -1.25 MPa for CT and -0.84 MPa for NT. Both treatments showed in general a similar daily course of PN1750, but much lower values for CT compared to NT. Highest PN1750 of DOY 221 occurred around 12 p.m. for both treatments, with a recorded maximum of 12.2 µmol m^{-2} s^{-1} for CT, and 16.6 µmol m^{-2} s^{-1} for NT. A visible drop of PN1750 occurred between 5:30 and 6:00 p.m. in both treatments, but was more profound in treatment NT. VPD and temperature were highest at 5:30 p.m. reaching 1.9 kPa and 25.8 °C, respectively. Photosynthetic active radiation had a maximum at 11:20 a.m., reaching 1443.6 µmol m^{-2} s^{-1}, and showed a variable daily course with sharp declines at 12:00 pm, 1:50 p.m. and 4:20 p.m..

In 2013, daily course of PN1750 has been recorded on DOY 157 for CT and NT in ‘Wellant’ (see Appendix Figure 35). Tree water potentials were not significantly different for NT and CT on this day (Ψ_{pd}: -0.11 MPa for NT and -0.1 MPa for CT; Ψ_{stem}: -1.2 MPa for NT and -1.3 MPa for CT). PN 1750 courses of CT and NT were quite similar for DOY 157, with clearly visible differences only between 4:00 and 7:00 p.m.. Highest mean photosynthetic rate of 19.2 µmol m^{-2} s^{-1} for NT was measured in the morning at 8:05 a.m., while highest rate for CT was 16.4 µmol m^{-2} s^{-1}, recorded at 9:15 a.m.. After reaching the maximum, PN1750 values gradually declined. Interestingly, in the late afternoon, NT showed lower PN1750 values than CT, while outer conditions remained similar. A maximum VPD of 2.6 kPa occurred at 3:40 p.m. and 4:50 p.m., while at the latter maximum temperature reached its daily maximum of 27.5 °C. Air temperature stayed above 20 °C from 8:40 a.m. until 7:50 p.m.. PAR consistently increased until the daily maximum value of 1838 µmol m^{-2} s^{-1} was reached at 12:40 p.m.. After this point PAR decreased and showed a large variability with changes of up to 1000 µmol m^{-2} s^{-1} difference in between 20 minutes (e.g. 2:30 p.m. to 2:50 p.m.) due to clouds.

Analyses of curve fitting parameter of all light response curves conducted in CT, NT and, ET in 2013 (on DOY 148, 156, 158, 162, 176, 189, 192, 196, 213, 234, and 241) were not able to detect statistically significant differences between treatments. Light response curves of 2012 were grouped according to their midday stem water potential (see Figure 16).

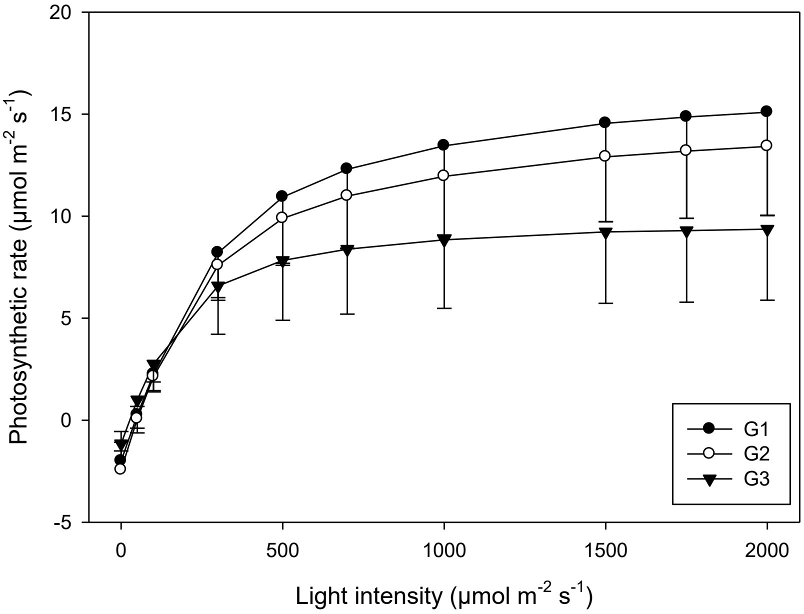

Figure 16: Light response curves of 'Wellant' leaves measured in 2012 grouped according to their midday stem water potential values (G1 (n=13): Ψ_{stem} > -1 MPa; G2 (n=18): -1 MPa > Ψ_{stem} > -1.5 MPa; G3 (n=9): Ψ_{stem} < -1.5MPa), error bars indicate standard deviations.

Statistically significant differences were found for calculated curve fitting parameter. Fitted maximum net photosynthetic rate, light compensation point, dark respiration and light saturation point were significantly higher in groups G1 and G2, compared to G3.

PN1750 measurements of 2012 and 2013, from 12 to 5 p.m., were grouped into seven groups (see Table 12) according to measured Ψ_{stem}, to allow statistical analysis.

Table 12: Average values and standard deviations of PN1750 measurements classified into seven groups according to their Ψ_{stem} values. Mean values (n=6-75) followed by a different letter in each column are significantly different at $p \leq 0.05$.

Group	Ψ_{stem} (MPa)	PN1750
1	*-0.5 to -0.75*	15.84 ± 2.3 a
2	*-0.75 to -1.0*	13.78 ± 2.4 ab
3	*-1.0 to -1.25*	13.81 ± 2.9 ab
4	*-1.25 to -1.5*	11.95 ± 3.2 bc
5	*-1.5 to -1.75*	9.18 ± 4.2 cd
6	*-1.75 to -2.0*	7.05 ± 2.5 de
7	*under -2.0*	5.49 ± 2.3 e

Between groups 1 to 3 (Ψ_{stem}: -0.5 to -1.25) no statistically significant difference was found. Group 4 was significantly different to group 1, 6 and 7, but not to group 2, 3 and 5. Group 5 was significantly different to all groups except 4 and 6, while group 6 was significantly different to all groups except 5 and 7. PN1750 measurements of plants with Ψ_{stem} under -2.0 MPa (group 7) was significantly different to all groups except group 6 (Ψ_{stem} from -1.75 to -2.0 MPa).

Photosynthetic rate between 12 and 4:30 p.m. decreases with lower Ψ_{stem} (Figure 17). An exact threshold could not be determined but at a Ψ_{stem} between -1 and -1.5 MPa net photosynthesis starts to decrease significantly. Average Ψ_{stem} values of the groups do not equal the middle of the range of the selected groups. A relationship between Ψ_{stem} and PN1750 is clearly visible, with lower Ψ_{stem} values leading to a reduced photosynthetic rate. A sigmoidal function ($y= 16.704/(1+\exp(-(x-(-1.714))/0.4267))$) was found by using the regression wizard of Sigma Plot with an R^2 of 0.9876.

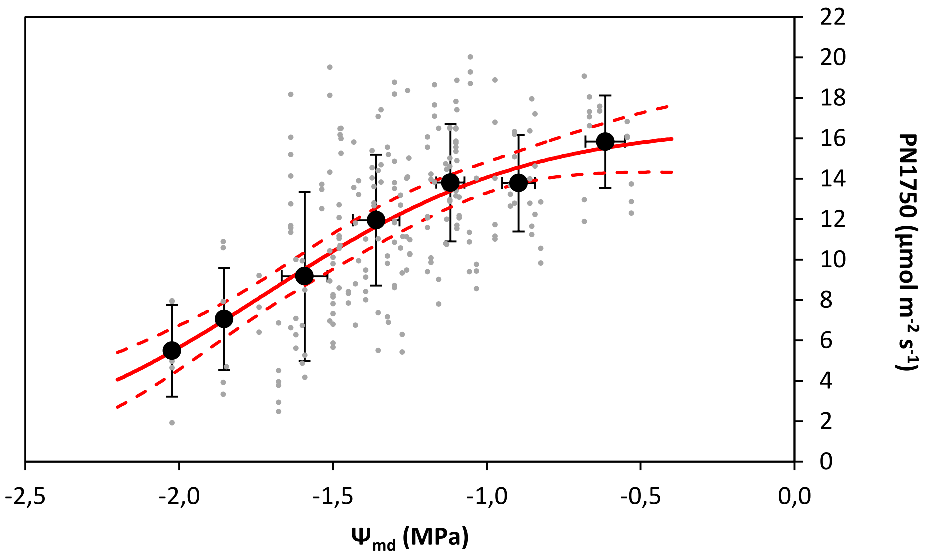

Figure 17: Single PN1750 measurements of 2012 and 2013 (12 to 4:30 p.m.) to corresponding Ψ_{stem} values (grey dots), used for statistical comparisons in groups. Additionally, average values (PN1750 and Ψ_{stem}) of used groups (black dots) (PN1750 measurements were grouped according to Ψ_{stem} values, with group 1: -0.5 to -0.75 MPa (n=16); group 2: -0.75 to -1.0 MPa (n=27); group 3: -1.0 to -1.25 MPa (n=62); group 4: -1.25 to -1.5 MPa (n=75); group 5: -1.5 to -1.75 MPa (n=47); group 6: -1.75 to -2.0 MPa (n=10); group 7: under -2.0 MPa (n=6)) with standard deviations (error bars) are presented. Average Ψ_{stem} values of groups are -0.61 MPa (group 1), -0.90 MPa (group 2), -1.12 MPa (group 3), -1.36 MPa (group 4), -1.59 MPa (group 5), -1.85 MPa (group 6), and -2.02 MPa (group 7). The sigmoidal function (y= 16.704/(1+exp(-(x-(-1.714))/0.4267)) (red solid line) with an R^2 of 0.9876 and the 95 % confidence band (red dashed line).

6.2.6 Harvest data

Harvest data are shown for all three cultivars and only for 2013, the first year with yield. In 2012, all fruits were taken of the trees directly after flowering.

6.2.6.1 'Jugala'

'Jugala' has been harvested on the 10th of September 2013 (DOY 253). Total fresh weight harvested per tree was significantly lower for CT, than for NT and ET (Table 13), while number of fruits per tree was similar between all three treatments.

Table 13: Harvest data of treatments CT, NT, and ET of 'Jugala' in 2013. Fresh weight per tree in kg (FW tree (kg)), number of fruits per tree (# Fruits/tree), and average fruit fresh weight (AvgFW/fruit (g)) calculated by number of fruits per tree and fresh weight per tree, were measured in the field. Mean values (n=12) followed by a different letter in each column are significantly different at $p \leq 0.05$.

Field	FW tree (kg)	#Fruits/tree	AvgFW/fruit (g)
CT	5.1 ± 0.56 a	30.8 ± 2.26 a	165 ± 15 a
NT	6.2 ± 0.65 b	32.6 ± 3.34 a	190 ± 7 b
ET	5.8 ± 0.60 b	29.9 ± 3.75 a	194 ± 13 b
Total	5.7 ± 0.75	31.1 ± 3.29	183 ± 18

Fresh weight of fruits measured in the laboratory was significantly different between all three treatments (Table 14). Additionally, a significant difference in starch rating for CT compared to NT and ET has been found. Firmness of ET, with the highest fruit fresh weight, was significantly lower than firmness of CT and NT. No difference between treatments has been found in soluble solids content for 'Jugala'. Malic acid content was similar between CT and ET, but was significantly higher in NT.

Table 14: Harvest data of treatments CT, NT, and ET of 'Jugala' in 2013, fresh weight per fruit (FW Fruit (g)), starch rating (1 - 10), firmness (kg cm^{-2}), soluble solids content (SSC(%)) and malic acid (g L^{-1}) were measured in the laboratory (60 fruit per treatment). Mean values (n=10) followed by a different letter in each column are significantly different at p ≤ 0.05.

Laboratory	FW Fruit (g)	Starch rating (1-10)	Firmness (kg cm^{-2})	SSC (%)	Malic acid (g L^{-1})
CT	172.4 ± 17.50 a	3.8 ± 1.06 a	9.6 ± 0.53 a	14.3 ± 0.77 a	4.4 ± 0.19 a
NT	189.6 ± 21.26 b	4.6 ± 1.67 b	9.7 ± 0.71 a	14.5 ± 0.86 a	4.7 ± 0.15 b
ET	203.0 ± 23.34 c	5.0 ± 1.34 b	9.4 ± 0.62 b	14.3 ± 0.77 a	4.4 ± 0.11 a
Total	188.4 ± 24.23	4.5 ± 1.47	9.5 ± 0.63	14.4 ± 0.80	4.5 ± 0.19

6.2.6.2 'Wellant'

Harvest of 'Wellant' was conducted on the 17th of September 2013 (DOY 260). CT had as for 'Jugala' significantly lower fruit fresh weight per tree. In contrast to 'Jugala', 'Wellant' had a significantly lower number of fruits per tree in CT than in NT and ET, while calculated average fruit fresh weight per tree was not different between treatments (Table 15).

Table 15: Harvest data of treatments CT, NT, and ET of 'Wellant' in 2013. Fresh weight per tree in kg (FW tree (kg)), number of fruits per tree (# Fruits/tree), and average fruit fresh weight (AvgFW/fruit (g)) calculated by number of fruits per tree and fresh weight per tree, were measured in the field. Mean values (n=12) followed by a different letter in each column are significantly different at p ≤ 0.05.

Field	FW tree (kg)	#Fruits/tree	AvgFW/fruit (g)
CT	2.97 ± 0.88 a	14.7 ± 4.48 a	203 ± 12 a
NT	5.80 ± 1.06 b	27.1 ± 5.17 b	215 ± 15 a
ET	4.96 ± 1.48 b	23.1 ± 8.25 b	204 ± 20 a
Total	4.52 ± 1.66	21.4 ± 7.96	207 ± 16

Fruits analyzed in the laboratory had significantly higher fresh weight in NT and ET than in CT (Table 16). No difference could be determined between treatments for starch rating and malic acid content. Firmness was significantly higher and soluble solids content significantly lower in CT compared to ET and NT.

Table 16: Harvest data of treatments CT, NT, and ET of 'Wellant' in 2013, fresh weight per fruit (FW Fruit (g)), starch rating (1 - 10), firmness (kg cm^{-2}), soluble solids content (SSC(%)) and malic acid (g L^{-1}) were measured in the laboratory (60 fruit per treatment). Mean values (n=10) followed by a different letter in each column are significantly different at p ≤ 0.05.

Laboratory	FW Fruit (g)	Starch rating (1-10)	Firmness (kg cm^{-2})	SSC (%)	Malic acid (g L^{-1})
CT	208.9 ± 22.98 a	5.1 ± 1.15 a	8.0 ± 0.57 b	16.3 ± 1.16 a	8.5 ± 0.63 a
NT	240.1 ± 29.14 b	5.2 ± 1.13 a	7.6 ± 0.54 a	16.7 ± 0.88 b	8.5 ± 0.58 a
ET	231.8 ± 39.50 b	5.6 ± 1.31 a	7.4 ± 0.41 a	16.8 ± 0.89 b	8.3 ± 0.98 a
Total	226.3 ± 33.45	5.3 ± 1.20	7.7 ± 0.58	16.6 ± 1.02	8.5 ± 0.72

6.2.6.3 'Sapora'

'Sapora' has been harvested on the 15th of October 2013 (DOY 288) and showed differing results to 'Jugala' and to 'Wellant'. Fresh weight harvested per tree significantly differed between the two irrigated treatments NT and ET, while CT showed intermediate behavior (Table 17). A significantly higher fruit number per tree was found for NT compared to ET and CT. Calculated average fruit fresh weight per tree was significantly lower in ET than in CT, while NT was intermediate. Fruit fresh weight of fruits analyzed in the laboratory was significantly lower for ET than for NT and CT (Table 18). Firmness, SSC and malic acid values showed no differences between treatments. For CT significantly lower starch rating has been measured than in ET and NT.

Table 17: Harvest data of treatments CT, NT, and ET of 'Sapora' in 2013. Fresh weight per tree in kg (FW tree (kg)), number of fruits per tree (# Fruits/tree), and average fruit fresh weight (AvgFW/fruit (g)) calculated by number of fruits per tree and fresh weight per tree, were measured in the field. Mean values (n=12) followed by a different letter in each column are significantly different at p ≤ 0.05.

Field	FW tree (kg)	#Fruits/tree	AvgFW/fruit (g)
CT	6.33 ± 0.95 ab	26.9 ± 5.25 b	234 ± 14 b
NT	7.14 ± 0.60 b	31.8 ± 2.41 a	224 ± 13 ab
ET	5.93 ± 1.07 a	27.4 ± 4.76 b	212 ± 11 a
Total	6.48 ± 1.00	28.7 ± 4.75	223 ± 15

Table 18: Harvest data of treatments CT, NT, and ET of 'Wellant' in 2013, fresh weight per fruit (FW Fruit (g)), starch rating (1 - 10), firmness (kg cm^{-2}), soluble solids content (SSC(%)) and malic acid (g L^{-1}) were measured in the laboratory (60 fruit per treatment). Mean values (n=10) followed by a different letter in each column are significantly different at p ≤ 0.05.

Laboratory	FW Fruit (g)	Starch rating (1-10)	Firmness (kg cm^{-2})	SSC (%)	Malic acid (g L^{-1})
CT	258.6 ± 27.88 b	5.3 ± 0.67 a	7.2 ± 0.63 a	17.0 ± 0.90 a	6.3 ± 0.45 a
NT	253.1 ± 28.45 b	5.9 ± 1.18 b	7.4 ± 0.49 a	17.0 ± 0.89 a	6.4 ± 0.51 a
ET	239.8 ± 28.22 a	6.1 ± 0.94 b	7.4 ± 0.65 a	17.1 ± 0.71 a	6.3 ± 0.48 a
Total	250.5 ± 29.12	5.8 ± 1.00	7.3 ± 0.59	17.0 ± 0.83	6.3 ± 0.47

6.3 Discussion of experimental results

6.3.1 Effects on tree development and phenology

The objective of the study was to investigate the effects of drip irrigation under German climate during the establishment phase of an orchard. Although the overall precipitation sums from April to October of both experimental years were higher than the 30-year average from 1981 to 2010 (DWD, 2011), the applied irrigation had an enormous measurable effect on tree development compared to the non-irrigated CT.

Higher total long shoot length was not primarily caused through a higher total number of long shoots, but through a longer total growth of single shoots. One reason for this was an extension of the growth period through irrigation and a later cessation of growth, especially in 2012. The result is in contrast to results of O’CONNELL et al. (2008), who observed no effect of irrigation treatments on seasonal shoot growth rate for mature trees and no prolonged growth period. Highest rates were measured at 26 DAFB and declined to near zero by 61 DAFB (O'CONNELL et al., 2008). Besides differences in weather conditions and differing behavior of cultivars, one reason for the discrepancy could be that shoots of young trees are thought to grow later in the season than shoots of mature trees (FORSHEY & ELFVING, 1989). PALMER (1988) also observed an earlier development of maximum leaf area as the trees aged.

A difference in the length of the growing period of the three cultivars could be one reason for the partly differing treatment results between cultivars. Differences in shoot growth of cultivars has been observed before (LAURI & KELNER, 2001). Another reason could be a general difference in water use and effects of water deficits. Differences in the ability of a given genotype to cease growth more or less rapidly under drought (LAURI et al., 2016) and the vulnerability to drought-induced embolism differed significantly between cultivars (BEIKIRCHER et al., 2013). Results of ‘Sapora’ 2013 additionally indicate that there exists a maximum possible vegetative growth, and above this point irrigation will not result in a higher vegetative growth. As a practical implication using irrigation much longer during a season may results in even longer shoot growth, but is not recommended because it could lead to problems with final bud formation. Cessation of shoot growth is important for bud organogenesis and therefore for the next season growth of the trees (LAURI et al., 2008).

Wood surface area was highly affected by additional irrigation compared to CT for all cultivars. This is in common with previous findings where water deficits were found to reduce radial trunk growth (IANCU, 1985; MILLS et al., 1996). Even late-season water deficits did limit the radial trunk growth in 'Braeburn' (MILLS et al., 1996), which also shows that radial trunk growth takes place until late in the season. Wood surface area is the result of vegetative growth of all previous years and thus part of the difference in 2013 might be explained by the carry-over of the first year differences. Besides the direct effect of the much higher long shoot length on wood surface area, presumably the higher leaf area in 2012 caused a higher overall assimilate production and a better start in 2013.

Compared to long shoot growth and wood surface area, number of spurs was less affected by irrigation. Spur development takes place very early in the season (FORSHEY & ELFVING, 1989), where usually no or only minor water deficits occur and therefore spurs were expected to be less influenced by irrigation. One reason for inconsistent effects between cultivars can be that number of spurs and of flowers is mainly influenced by the genetics of the scion (DENNIS, 2000), and cultivars might react differently to water supply. Since flowering also takes places early in the season and is mainly supported by reserves, no direct effect of irrigation was expected. However, this may change if there are multiple years of water deficits. Higher total flower numbers in NT than in CT in 2013 are likely to be caused by the significantly bigger tree size and a higher assimilation of reserves of the irrigated trees in 2012. Enhanced (IANCU et al., 2011) and reduced (KILILI et al., 1996a; BEHBOUDIAN et al., 1998) flower numbers in the season following a deficit irrigation have been reported for apple trees. One possible explanation for the contradictory results may be a difference in the intensity and timing of water deficits. Early deficits were found to significantly reduce return bloom (KILILI et al., 1996a). Water deficits in 2012 might have affected flower induction of CT in 2012, but since all fruits have been removed early in 2012, competition for carbon and therefore resulting carbon deficit for flower induction is expected to be negligible.

Overall, results indicate a high effect of additional irrigation and water deficits on vegetative growth during the early years of apple orchard establishment for German conditions. In addition, results imply that water deficit effects on spur and flower development are related to indirect effects of carbon supply and partitioning. Varying results between cultivars also indicate differences in water use of apple cultivars, which might also partly explain contradictory results in the literature. Weather conditions highly affect the effects of irrigation on apple tree development and with a high amount of precipitation, irrigation effects become less significant. At a specific point more water does not necessarily lead to a higher growth. But the results also indicate that a fast growth in the first year caused by a good water supply in ET and NT compared to a lower water supply in CT can still be visible and relevant in the following years and thus lays the basis for a faster establishment of young orchards. In terms of the original objective, results are even more important, since the two experimental years were even wetter than the average. Monthly average temperatures were similar between 2012 and 2013 and also comparable to 30-year monthly average temperatures for Geisenheim (DWD, 2011), exceptions from this are May and August 2012 and July 2013. Both measurement years showed hotter periods (higher maximum temperatures, higher monthly average temperatures, and more summer days) than the 30-year temperatures from 1981 to 2010 (DWD, 2011), which is one reason for the high effects in spite of the higher than usual precipitation. Due to the Changing Climate it is expected that during the growing period less overall precipitation and longer periods without rain will occur (STÖCKLE et al., 2011). These conditions will highly enhance positive effects of additional irrigation on the vegetative growth of apple orchards. On a physiological point of view, additional irrigation is very beneficial under German conditions and can be highly recommended for new orchards.

6.3.2 Light interception

The high effect of additional irrigation on tree growth was also visible in light interception measurements of trees. The % LI value of CT in 2013 has already been reached in 2012 by the two irrigated treatments. In 2013, midday LI of CT was about 17 %, while NT and ET showed values around 24 % in their third year. Results are comparable to trials conducted in Spain (GIRONA et al., 2011) and in general appropriate for young trees. Effects of irrigation and water deficits on vegetative growth and LI of apple trees are well known (JACKSON, 1980; FORSHEY & ELFVING, 1989; EBEL et al., 1995; FERNANDEZ et al., 1997b; O'CONNELL & GOODWIN, 2007). LI is related to vegetative growth of apple trees and thus related to available water in young trees, but water use of apple trees is also related to total LI (JACKSON, 1980; AUZMENDI et al., 2011).

In the current case, differences between ET and NT in timing, used irrigation system, and even total irrigation amount had no clearly measurable effect on LI. But although not statistically significant, NT, which had a higher total irrigation amount than ET, had in average a slightly higher LI and differences might be more profound under dryer conditions. Compared to values for mature trees (PALMER, 1989b; CASADESUS et al., 2011) trees of ET and NT already reached two thirds of the LI in their third year, while non-irrigated CT trees did not even reach half. This indicates the importance of maintaining good water supply in the early years when vegetative development is critical compared to mature trees where reproductive performance is needed.

For the calculation of long shoot leaf area per tree, a relationship between shoot length and leaf area has been used. JOHNSON and LAKSO (1985) found very good linear relationships ($R^2 > 0.88$) between leaf area and shoot length. They also found differences in this relationship between cultivars. In the current case, differences between 'Jugala', 'Sapora' and 'Wellant' were visible but not very profound. The used linear relationship for 'Wellant' only had an R^2 of 0.74 and therefore extrapolation of total leaf area is afflicted with some uncertainty. In addition, no linear relationship between leaf area and spur length has been found, which corresponds to previous findings (ROM & BARRITT, 1990). Although long shoot length was only statistically significantly different on a 10 % level between irrigated and non-irrigated treatments, and number of short shoots was not statistically significantly different between CT and ET, overall calculated leaf area was significantly different between CT and the two irrigated treatments. LI of spurs and long shoots is known to differ between cultivars and training systems, and total LI is the result of intercepted radiation of spurs and long shoots (and of wood structures) (JACKSON & PALMER, 1980; WÜNSCHE & LAKSO, 2000; CORELLI-GRAPPADELLI, 2003). Although not statistically significant, CT trees had the lowest total long shoot length in addition to the lowest number of spurs in 2013. Total leaf area calculation combines the single length of all long shoots and the number of spurs per tree. Overall, calculated total leaf area corresponded well with measurements of LI. Total leaf area calculation has been used to calculate leaf area index (LAI). LAI of NT was nearly twice the size of CT, which additionally shows the advantage of NT trees compared to CT. For mature apple trees, a LAI between 1.8 and 3.6 has been reported (JACKSON, 1980; WÜNSCHE et al., 1996; WÜNSCHE & LAKSO, 2000), depending on rootstock, planting and training system. Compared to this, calculated LAI values are very low. But the trees were still in the establishment phase and thus LAI values cannot be easily compared to values of mature orchards of differing growing systems.

Overall, even in relatively wet years, the measured LI and the calculated total leaf area show that vegetative development of the experimental apple trees was much higher for irrigated than for non-irrigated trees. A higher LI gives the irrigated apple trees the advantage of being able to assimilate more carbon (irrespective of effects on photosynthesis itself). Thus they accumulate more assimilates for growth, which additionally can lead to a faster development and establishment of the trees.

6.3.3 Water potential

The Ψ_{pd} values are similar to values reported by others (MILLS et al., 1997; DOLTRA et al., 2007; LEBESE et al., 2008) and generally in a common range. Some differences between NT and ET might be explained by differences in irrigation timing and amount. But no clearly detectable unique effect of one of the two different irrigation systems on the seasonal course of Ψ_{pd} in the conducted experiment was seen. Termination of irrigation in both treatments led to a similar curve progression of Ψ_{pd} in both years. This indicates that water availability to the tree roots in the soil was similar. Ψ_{pd} results generally corresponded to soil based measurements.

Similar to the current results, Ψ_{pd} and Ψ_{stem} measurements of DOLTRA et al. (2007) showed dissimilar seasonal courses. But current measurements of photosynthesis did not correspond with Ψ_{pd} measurements (see Appendix Figure 37). Although Ψ_{pd} has been proposed as a primary water stress indicator in trees (SIRCELJ et al., 2007), results indicate that Ψ_{pd} only corresponds to water availability to the tree from the soil during the night, but is not a reliable indicator for daytime water status and for processes that take place in the light period like photosynthesis. Experimental trees were planted in 2011 and root density and distribution were supposed to be still low. The Ψ_{pd} value of -0.25 MPa of NT and ET could be used as a reference line for irrigation, but this is not recommended due to the problems connected to using Ψ_{pd} as a water status indicator in heterogeneously wetted soils. For many annual crops and for young fruit trees grown in containers, Ψ_{pd} was assumed to represent the mean soil water potential next to the roots (AMÉGLIO et al., 1999). Differing experimental results for Ψ_{pd} have led to discussions about whether it represents the wettest, the average, or the driest zone of the soil (VALANCOGNE et al., 1997; AMÉGLIO et al., 1999). AMÈGLIO et al. (1999) concluded, that in heterogeneous soils, plants tend to equilibrate its Ψ_{pd} nearer to the wettest zone of the soil than to the driest (AMÉGLIO et al., 1999), while under homogenous soil water conditions Ψ_{pd} can be taken as a measure for soil water potential (COHEN & NAOR, 2002). A small volume of wet soil can re-hydrate the tree at night when there is little or no waterloss, thus giving a high $\Psi_{pd.}$ However in mid-day with high transpiration, a small wet soil volume will not be able to maintain tree water supply. While Ψ_{pd} has been found to be in correlation with soil water content, Ψ_{stem} was found to be a sensitive measure of plant water status throughout the entire day in apple (NAOR et al., 1995). NAOR and COHEN (2003) regarded Ψ_{stem} to be an indicator of the maximum daily plant water stress. The current results support the hypothesis of AMÉGLIO et al. (1999) for heterogeneously wetted soils.

Similarly, in an experiment by ZHAO et al. (2006) with a non-stressed control (CK), a half root stress (HRS), and a whole root stress (WRS) treatment, no significant difference between CK and HRS has been found for Ψ_{pd}, while Ψ_{pd} was significantly lower in WRS.

Interestingly, diurnal leaf water potential of HRS was lower than CK and higher than WRS during most of the daytime. Additionally, photosynthetic rate of HRS was lower than that of CK (ZHAO et al., 2006). This also shows that for apple photosynthesis, daytime water status measurements might be a better indicator. In addition, results indicate that although trees might be able to collect enough water during the night, water uptake limits may occur during the daytime and photosynthesis might be affected. One possible explanation for this is the use of dwarfing rootstocks in modern apple production, which were found to have a low hydraulic conductivity (ATKINSON et al., 2003).

Seasonal courses of Ψ_{stem} measurements showed a higher variability than Ψ_{pd} measurements. Additional influencing factors are temperature and humidity during the day. Ψ_{stem} results display that irrigation has led to effects in the experimental trees and it is visible that general water supply was different between 2012 and 2013, with 2013 being a wetter year.

A visual comparison between water potential measurements and gas exchange measurements shows that Ψ_{stem} seasonal curve corresponds better to seasonal curve of Pn values than Ψ_{pd} does (also see Appendix Figure 37 and Figure 38). In contrast to DOLTRA et al. (2007), no relationship between Ψ_{pd} and photosynthesis measurements has been found in the current data. Mean measured Ψ_{stem} values during 2012 and 2013 were in a range between -0.5 and -2.0 MPa. Ψ_{stem} is known to be a suitable indicator for apple tree water status and has been used by several authors (BEHBOUDIAN et al., 1994; EBEL et al., 1995; EBEL et al., 2001; COHEN & NAOR, 2002; NAOR & COHEN, 2003; REYES et al., 2006; DOLTRA et al., 2007; O'CONNELL & GOODWIN, 2007; DE SWAEF et al., 2009; GIRONA et al., 2010; AUZMENDI et al., 2011; BEHBOUDIAN et al., 2011; GARCÍA PETILLO et al., 2011; GONZÁLEZ-TALICE et al., 2012). AUZMENDI et al. (2011) measured Ψ_{stem} values down to about -1.0 MPa for fully irrigated apple trees and values down to -1.4 MPa during drought cycles. They also found a linear relationship between transpiration and Ψ_{stem}, and calculated zero transpiration to occur at a Ψ_{stem} of -2.6 MPa. CASADESUS et al. (2011) reported similar values of Ψ_{stem} in the range between -0.6 MPa and -1.3 MPa. Slightly lower values have been reached in experiments conducted by NAOR and COHEN (2003) (range from -0.8 to -1.5 MPa), and by DOLTRA et al. (2007) (range from -0.6 to -1.73 MPa). The Ψ_{stem} values measured in the presented experiment in Geisenheim are in the same range and thus plausible. Severe water stress is supposed to occur at values below -2.0 MPa (NAOR, 2006). In a semi-arid region in Israel, measured Ψ_{stem} varied from -0.9 down to -2.8 MPa (NAOR et al., 2008). Lower values for apple trees have only been reported for potted apples (range between -0.5 and -4.5 MPa)(DE SWAEF et al., 2009). These authors presented a Ψ_{stem} threshold of -1.1 MPa for reduction of maximum photosynthetic rate. They also found a better relationship of maximum photosynthetic rate with Ψ_{stem} than with maximum daily trunk shrinkage. NAOR and COHEN (2003) reported higher standard deviations, and thus a higher variance, in the stressed than in the non-stressed treatment, which has also been seen in the current experiment.

Although Ψ_{stem} is thought to be one of the best indicators for plant water stress, it also is affected by different factors, e.g. temperature and humidity. Lower Ψ_{stem} values are expected at high crop loads (BERMAN & DEJONG, 1997; NAOR et al., 1997; NAOR et al., 2008). But also on the contrary, fruit size and quality is affected by low Ψ_{stem} (NAOR et al., 1995; MILLS et al., 1996; MPELASOKA et al., 2000b). O'CONNELL and GOODWIN (2007) found a good linear relationship between Ψ_{stem} and VPD. Water status and plant transpiration in apple orchards can be more influenced by atmospheric conditions than by soil moisture due to its relatively small root biomass and relatively high hydraulic resistance (LANDSBERG & JONES, 1981; LAKSO, 1994). This has also been visible in the current study. Ψ_{stem} has been found a good plant water stress indicator for irrigation scheduling in fruit trees (NAOR, 2000). This also implies that plant based measurements are possibly more important than soil moisture measurements to control tree water status (DOLTRA et al., 2007). Plant based water status indicators have the advantage to integrate climatic and soil conditions. Plant based sensing allows a faster detection of suboptimal watering conditions and is less influenced by other factors (DE SWAEF et al., 2009). But direct plant sensing can be very sensitive. A disadvantage of plant based water status indicators is, that they do not tell the grower how much water has to be applied as it is a measure of water status, not water use (JONES, 2004). Therefore, plant based indicators require the definition of threshold values. For many cases it is helpful to identify a general reference point of water stress (BRADFORD & HSIAO, 1982), e.g. the level of water stress that induces a significant change of the monitored process. A Ψ_{stem} of about -1.5 MPa is thought to be an indicator of moderate water stress in fruit trees (MARSAL et al., 2004; AUZMENDI et al., 2011). But plant based water status indicators show a high day-to-day variability due to their response to environmental conditions and a fixed threshold may lead to errors in irrigation. Additionally a high tree-to-tree variability has been reported (NAOR & COHEN, 2003), which would make a thoughtful selection of reference trees in the orchard extremely important. These are some of the reasons why plant based sensing techniques are mostly used in research and are mainly still under development. Ψ_{stem} is a direct water status indicator and thus more easily transferable, e.g. across the growing season, or between sites (DE SWAEF et al., 2009), but it is very time consuming, labor intensive, destructive and non-automatable. The development of a non-destructive and automatable plant water status sensor would highly improve this kind of plant measurements and the whole problem of irrigation scheduling.

6.3.4 Photosynthesis

6.3.4.1 PN1750

Mean PN1750 rates were comparable to the ones found by KILILI et al. (1996b) for the cultivar 'Braeburn'. They found a significant linear relationship between Pn and stomatal conductance, but also reported that other factors (assimilate accumulation or decreased activity of photosynthetic enzymes) must have contributed to reductions of Pn in the water-stressed trees (KILILI et al., 1996b). A linear relationship between Pn and stomatal conductance has also been found by LAKSO (1994), WÜNSCHE et al. (2005) and LAKSO (2014). Presented experimental photosynthetic rates are in a normal range for healthy apple leaves (FLORE & LAKSO, 1990; KILILI et al., 1996b; MIEROWSKA et al., 2002; LOMBARDINI et al., 2004; MASSONNET et al., 2007; SIRCELJ et al., 2007; LEBESE et al., 2008; DE SWAEF et al., 2009). Literature data also imply that photosynthetic rates do not differ much between cultivars. This also corresponds to findings of this study, where no difference in photosynthetic rate between cultivars grown in Geisenheim has been found. Special emphasis is given to the direct comparison between 'Sapora', which is a triploid apple cultivar, and 'Wellant', a diploid cultivar. PN1750 of non-stressed trees of both cultivars, measured on the same days in 2013, did not differ significantly. There is no indication that photosynthetic rate differs between cultivars.

Water status and especially water deficit is known to affect photosynthetic rate of apples, as also has been seen in the experiment. Apple leaf photosynthesis declines with developing water stress (LANDSBERG & JONES, 1981). But mature apple leaves have been found to be able to adjust osmotically (LAKSO et al., 1984) by the accumulation of monosaccharides, especially sorbitol (WANG & STUTTE, 1992). Osmotic adjustment allows turgor maintenance and thus helps to maintain gas exchange longer during water deficit conditions. The presented seasonal photosynthetic rates do not indicate that osmotic adjustment took place during the season, but no analysis of leaf contents has been conducted. SRITHARAN and LENZ (1989) and LOMBARDINI et al. (2004) also found that irrigation led to significantly higher leaf photosynthetic rates on some measurement days in fully irrigated treatments for fruiting apple trees. This also indicates that water deficits reduce maximum possible photosynthetic rates. The effect of developing drought stress on photosynthesis has been found to be a result of stomatal closure as well as non-stomatal limitations (metabolic impairment) (FLORE & LAKSO, 1990; LAWLOR, 2002; MEDRANO et al., 2002). Stomatal closure is one of the first reactions during the development of water stress and metabolic impairment occurs during longer drought periods and during higher levels of water stress (JONES et al., 1990). Additionally, it is known that both, soil and also atmospheric water deficits do have an effect on photosynthetic rate in apple. NAOR (2000) found Ψ_{stem} to be correlated with stomatal conductance in apple (R^2 of 0.85), in the range from -0.7 MPa to -1.6 MPa (g_s from 0.3 to 0.1 mol m^{-2} s^{-1}). Internal CO_2 (C_i) is a useful indicator of whether stomatal or non-stomatal factors affect photosynthetic rate (FLORE & LAKSO, 1990). Typically, C_i is about 70% of the ambient concentration in C_3 leaves at high light conditions (TIMLIN et al., 2008). For the obtained data of 'Wellant', C_i decreased continuously with decreasing stem water potential down to -1.8 MPa, but visibly increased for stem water potentials below -2 MPa (data not shown). The first decrease in C_i indicates that photosynthetic rate was mainly affected through stomatal effects, and the range agrees with the above mentioned results of NAOR (2000). The increase of C_i at water potentials below -2 MPa indicates that at this point also non-stomatal factors start to affect photosynthesis of apple leaves. KILILI et al. (1996b) reported that a reduction in photosynthetic rate in a non-irrigated treatment was not solely caused through stomatal but also through non-stomatal mechanisms. SIRCELI et al. (2007) also reported stomatal limitations of photosynthesis under moderate drought, and in addition non-stomatal ones under a severe drought. In contrast, MILLS et al. (1996) suggested a stomatal regulation of Pn under water stress conditions, because C_i values were not affected. Possibly, stress was not severe enough to induce non-stomatal limitations.

Overall, photosynthetic rate of mature apple leaves is thought to stay similar during the season (FLORE & LAKSO, 1990). In the presented results of 2012 and 2013 some major drops in PN1750 were visible, but are not thought to be caused by a general seasonal Pn pattern. Over the season 2012 three days (DOY 180, 207, and 254) showed noticeable low PN1750 values in all three treatments. These drops can also be seen in Ψ_{stem} values of the same days, but except for DOY 254 not in Ψ_{pd} values. Besides water status of the tree which is supposed to have the main effect, some additional factors are supposed to be involved in these drops. Maximum temperature exceeded 30 °C and maximum VPD also showed high values (DOY 180: 3.1 kPa; DOY 207: 4.1 kPa; DOY 254: 3.6 kPa). These high temperature and high VPD values probably led to reduced PN1750 rates compared to other measurement days. The used gas exchange measurement system is only able to change outer conditions in a specific range. Optimum temperature for apple leaf photosynthesis has been found to be between 25 and 35 °C (WATSON et al., 1978; GINDABA & WAND, 2007; FAN et al., 2010), dependent on temperature conditions during development (FAN et al., 2010). Besides temperature also VPD can have an effect on photosynthetic rates of apple leaves. Stomatal conductance is known to be affected by VPD, but a simple linear relation has been questioned (JONES, 1985). At low VPD levels, stomatal opening of apple leaves is thought to be mainly affected by photosynthetic rate (dependent on radiation and temperature), while, at higher VPD levels (> 2,5 kPa (JONES et al., 1985)), stomatal response to VPD is thought to become the limiting factor (DRAGONI et al., 2004). When comparing full day measurements of PN1750 of 2012 and 2013 of NT it can be seen that the higher VPD values in 2013 led to a lower PN1750 during the afternoon, while radiation and temperature conditions were similar between the two days. This also indicates a high influence of VPD on apple photosynthesis. Interestingly, full day measurement in 2012 showed that the general daily PN1750 pattern of CT and NT was also similar, but values of CT were lower by about 5 µmol m^{-2} s^{-1} during the whole day. In 2012, Ψ_{pd} and Ψ_{stem} were significantly lower in CT than in NT. The difference of PN1750 between NT and CT stayed similar during the day, instead of showing a similar increase in the morning, followed by an early decrease in CT than in NT, which we first expected. The results indicate that photosynthesis of water stressed trees do not start similar to non-stressed ones and then decrease their photosynthetic rate at some point during the day. Instead whole day photosynthesis seems to follows a similar pattern but is reduced by a specific portion, at least for soil based water deficits.

6.3.4.2 Light response curves (LRCs)

Like for PN1750 measurements, light response curve measurements were not able to detect differences between apple cultivars. But for LRCs of ‘Wellant’, grouped by Ψ_{stem}, significant differences were found between groups. LRCs measured by MIEROWSKA et al. (2002) for spur leaves of summer pruned ‘Golden Delicious’ trees are very similar to the LRCs of group 1 and 2 measured in ‘Wellant’, while curves of ‘Granny Smith’ showed slightly lower maximum Pn values. Presented LRCs are also very similar to LRCs measured in ‘Braestar’/M25 at 25 °C by PRETORIUS & WAND (2003). They also reported differences of LRCs measured pre- and postharvest at different temperatures, but did not measure water status of the trees. Optimum temperature for photosynthesis was 25 °C pre- and postharvest, with pre-harvest optimum range being 25 to 30 °C, and post-harvest optimum range being 20 to 25 °C (PRETORIUS & WAND, 2003). JONES & FANJUL (1983) measured LRCs in water stress (S1 & S2) and an irrigated control (C) treatments. They found maximum photosynthetic rate to be decreased in the stress treatments, while CO_2 compensation point tended to decrease with medium stress (S1) and increase with greater water stress (S2). Midday leaf water potentials were -1.1 MPa for C, -1.7 MPa for S1 and -2.7 MPa for S2 treatment (JONES & FANJUL, 1983). In the presented LRCs for 'Wellant' a decrease of compensation point for plants under water stress has been found, like in S1. But no increase, like in S2 of JONES & FANJUL (1983), was visible. A reason for this might be a higher water stress level in S2 (JONES & FANJUL, 1983) than in the current experiment, but midday leaf water potentials and midday stem water potentials cannot easily be compared.

6.3.4.3 Relationship between stem water potential and photosynthetic rate

Experimental results of PN1750 and LRC measurements showed that photosynthetic rate declined with declining Ψ_{stem}. The results agree with data obtained by DE SWAEF et al. (2009) and STEPPE et al. (2008) where measurements were conducted in only one potted apple tree per treatment. Such data are, however, difficult to interpret since potted trees have been found to react differently than field grown ones and one tree per treatment is not sufficient. The response of photosynthetic rate to Ψ_{stem} was described by a sigmoidal function (R^2 of 0.973) for the non-irrigated tree (STEPPE et al., 2008). The function itself has not been published and therefore cannot be directly compared to the found sigmoidal function (R^2 of 0.9876) for PN1750 of field growing apple trees of the cultivar 'Wellant', but showed a similar course with a slightly stronger sigmoidal shape. Reference values for a threshold were found to be between -1 MPa (STEPPE et al., 2008) and -1.16 MPa (DE SWAEF et al., 2009). This approach is similar to a critical reference value determination often used for fruit tree irrigation, by taking measured values of fully irrigated trees (JONES, 2004). Reference values determined for irrigation of apple trees range between -1 MPa (NAOR & COHEN, 2003) and -1.5 MPa (DOLTRA et al., 2007). Additionally thresholds are determined empirically and transferability to other orchard situations is unclear, but are suggested to be transferable among orchards on a within-region basis (NAOR et al., 2008). Water potential reference values for photosynthesis of irrigated trees might also vary between potted and orchard grown apple trees. In the presented data for 'Wellant' a possible threshold value based on the grouping of PN1750 measurements appears to be slightly lower than the ones reported by STEPPE (2008) and DE SWAEF (2009). When taking only the upper limit of data (see Appendix Figure 36), since it is not reasonable to assume that the low PN1750 values are caused by the water potential, an even lower threshold of -1.6 MPa is visible. But measurements were conducted during the whole season and osmotic adjustment might have occurred, which is thought to lead to a shift of the threshold to a more negative value. Therefore, for now, the grouped data threshold appears to be more reasonable.

Overall, experimental results support some hypotheses of earlier experiments, e.g. a strong influence of water status on photosynthetic rate of apple trees has been found. Besides soil water deficits also VPD influenced photosynthesis. Midday stem water potential appeared to be a good water status indicator for apple trees and in particular for water deficit effects on photosynthesis. Results also confirm the advantage of using plant based water status indicators instead of only measuring soil moisture. Although experimental results were able to approve some previous assumptions it is evident that there still exist some major gaps in the understanding of apple photosynthesis itself, and of the exact impacts water deficits on photosynthesis. This demonstrates the need for future research in respect of achieving a comprehensive understanding of apple photosynthesis, including establishing trees, soil and air water deficits, stomatal and non-stomatal limitations, osmotic adjustment, build-up of leaf starch, and during the whole day and season.

6.3.5 Harvest

Harvest data of the three cultivars showed a diverse picture and cannot be easily generalized. Possible reasons for the inconsistent results among the three cultivars might be due to their varying ripening times and thus varying harvest dates (including different weather conditions during ripening), due to their inherent fruit size differences, due to unbalanced thinning or caused by other unknown factors. In 2013, flower number might have been affected by water deficits and establishment of trees in 2012. Additionally, the trees were still very small during the measurements and it was the first harvest. All three cultivars came from different nurseries and pretreatment of trees before planting in the orchard, although not very likely, might also have had an influence.

In 'Jugala', irrigation treatments led to the expected significantly higher fruit fresh weights and also to an earlier ripening than in CT. The earlier ripening of NT and ET fruits was also visible for 'Sapora'. For unknown reasons, fruits of ET of the latest ripening cultivar 'Sapora' were significantly lighter than the ones of NT and CT. Harvest data of 'Wellant' showed significantly lower values in CT than in NT and ET for total fresh weight per tree and number of fruits per tree. Trees were hand thinned to 30 fruits per tree after flowering, but for unknown reasons CT trees only had an average of 14.7 fruits per tree at harvest. Possible reasons could be the reduction of fruits during June drop, or a biased handthinning. The average fruit fresh weight did not differ between treatments, probably due to the reduced number of fruits per tree in CT. But randomly selected fruits of CT analyzed in the laboratory were significantly lighter than fruits of ET or NT. While starch index and acidity did not differ between irrigation treatments, CT fruits showed significantly lower soluble solids content and higher firmness compared to NT and ET.

Firmness depends on fruit size, which also was significantly lower in CT, and might not be caused by water deficits itself but by smaller fruits in the sample. SSC of CT was 0.4 % lower than in NT and showed a high standard deviation. Mid to late season water deficits in CT might have led to reduced SSC caused by decreased photosynthetic rates. Smaller tree sizes and thus smaller leaf area for CT might also be involved.

Numerous literature reports on the effect of reduced irrigation on yield and fruit quality of apple exist, but also often present contradictory results as seen in the current study. Water stress occurring early in a season can lead to a reduced return bloom in the next season (KILILI et al., 1996b). Water stress effects on fruit yield and quality are known to depend on crop load of trees (MPELASOKA et al., 2001; NAOR et al., 2008). In general, fruit size in apple is thought to decrease with application of deficit irrigation, especially if more severe water stress develops (BEHBOUDIAN et al., 2011). Various deficit irrigation treatments reduced average fruit weight compared to fully irrigated treatments (GIRONA et al., 2010), which in the current case was only clearly seen for 'Jugala'.

Fruit firmness is influenced by fruit size, with smaller fruits generally being firmer than larger fruits (EBEL et al., 1993). Some contradictory results about how DI, RDI and PRD compared to full irrigation affects apple fruit firmness have been reported. Fruit firmness results should be treated with caution. As already mentioned fruit size influences fruit firmness, but also ripening stage of the fruit has an effect on firmness of fruits. Increased maturity leads to softer fruits. Some studies considered these points and divided harvested fruits in groups according to their size. Fruit firmness of deficit irrigation treatments was found to be higher than in fully irrigated treatments for 'Fuji'/unknown rootstock (LEIB et al., 2006) and for 'Braeburn'/MM.106 (MPELASOKA et al., 2000a; MPELASOKA & BEHBOUDIAN, 2002). For 'Pink Lady', on MM.106 and on M.9, no effect of deficit irrigation treatments on fruit firmness has been detected (O'CONNELL & GOODWIN, 2007; TALLUTO et al., 2008). ZEGBE & SERNA-PÉREZ (2011) used commercial irrigation and PRD for 'Golden Delicious' on M7 in a semi-arid region and found no differences in flesh firmness and total soluble solids concentration. Only in dry matter concentration differences were detected.

Like for fruit firmness also for total soluble solids, experimental results vary between studies. Significantly higher Brix values for fruits of deficit irrigated than of fully irrigated treatments were measured in 'Fuji' (LEIB et al., 2006) and in 'Braeburn' (MPELASOKA & BEHBOUDIAN, 2002). For 'Pink Lady' no statistically significant difference between treatments was found for total soluble solids (O'CONNELL & GOODWIN, 2007; TALLUTO et al., 2008). BEHBOUDIAN (1998) reported enhanced total soluble solids for deficit irrigated treatments (14.7 ° Brix) compared to fully irrigated treatments (13.7 ° Brix) for 5-year old 'Braeburn'/MM.106 growing in lysimeters. Also for titratable acidity, experimental results are very dissimilar. MPELASOKA & BEHBOUDIAN (2002) reported higher starch pattern index values for a fully irrigated treatment than for a deficit irrigated treatment in 'Braeburn', which indicates a faster ripening under stress conditions. Experimental differences between fully and deficit irrigated treatments show high variability between seasons (LEIB et al., 2006). LEIB et al. (2006) found differences in soluble solids content for varying irrigation treatments only in two out of three years.

Possible explanations for inconsistencies among studies might be differences between cultivars, differences in timing of deficit irrigation or in water stress intensity during experiments. Overall, results are difficult to compare due to too many influencing effects and thus possible differences between experiments in respect to amounts of rainfall, irrigation, weather conditions and soil water reserves. All examined studies were conducted in mature apple trees. The results of this study were collected in newly planted apple trees and first harvest results should not be over-interpreted. Overall, no extreme differences between CT, NT, and ET fruits were found, but the year was wetter than the average and therefore effects are expected to be clearer during average and especially for drier years. In 2013 irrigation only led to higher yields analyzed as total fresh weight per tree, but fruit numbers per tree were much lower in CT than in NT. It partly remains unclear if differences of treatments were caused through irrigation treatments in 2013 or partly already through pre-conditioning in 2012, or through other unknown factors.

6.3.6 Soil moisture measurement

The use of different dripper systems has led to some issues concerning soil moisture measurement positions. Especially in NT with only one single dripper per tree the distance from the soil moisture measurement system to the dripper plays a major role for reliable measurements. This circumstance also makes it very difficult to achieve reliable results of soil moisture with only a few soil moisture, because selecting a sensor position that is representative of the root-zone is difficult (JONES, 2004). If sensors are placed directly beside the dripper, they will most of the time record very high moisture levels although the tree might not necessarily be able to reach most of the moisture. In case they are placed too far from the drippers, soil moisture sensors are likely to record very dry conditions although the tree might still have access to sufficient water. LEVIN et al. (1979) measured soil moisture content in several distances from single drippers and showed that soil wetting and drying, and also soil water content, varies with distance. This is especially true for the uppermost soil layers and should be kept in mind when soil moisture data is analyzed. The use of three different soil moisture sensors has the advantage that the systems themselves can be compared, and also that problems of one measurement technique may not be present in the others. But in the current case it also had the disadvantage of having only a small number of sensors per measurement system in each treatment.

Results of 2012 show that precipitation events have been clearly visible in tensiometer measurements of 25 cm depth in CT. Recorded higher amounts of precipitation led to an increase of values, while lower precipitation amounts led to stable values. In 50 cm depth, also higher precipitation amounts only led to a less steep decline of tensiometer values in CT. Rain events in 2012 were not able to provide enough water in 25 and 50 cm to preserve a certain level of soil moisture. The soil dried out in both layers during the season, which indicates that the tree roots were able to extract water from both depths. Besides precipitation, irrigation events of ET and NT were visible in 25 and 50 cm depth. This shows that irrigation was able to refill soil water down to over 50 cm depth. After irrigation treatments have been stopped for the season, a dry out has been visible in the tensiometer values measured in both depths.

It is unclear why the first very negative values of NT (between DOY 120 and 128) have developed, because irrigation in NT started on DOY 116 in 2012 and the measured tensiometer values were much more negative than the ones in the non-irrigated treatment CT. This could have been caused by a measurement error or by a very unfortunate positioning of the tensiometers in 25 cm depth in NT. Values between single tensiometers also varied extremely in NT. Furthermore, NT values in 50 cm depth provide evidence for one of the mentioned explanations. In 50 cm depth both irrigated treatments NT and ET showed soil moisture tensions between -90 and -250 hPa during the whole irrigation period in 2012, which is in a recommended range for growers (IMMIK, 2008), and no major water deficits should occur. Additionally, a clear increase of values was visible in the course of both treatments after irrigation has been started.

In 2013, higher correlation coefficients were found between 25 and 50 cm depth than in 2012, which is probably caused by the more periodic and higher amounts of rain. Efficient rainfalls soak the soil more equally than the dripper irrigation systems. Even in the non-irrigated CT soil moisture stayed on a high level from DOY 95 until about DOY 175 in 50 cm depth. The values in 25 cm depth were very variable in 2013, but irrigated treatments showed higher soil moisture levels through most of the season. Tensiometer measurements also showed that the non-irrigated soil of CT dried out more slowly in 2012, while in 2013 a much faster drying was visible for the tensiometer measurement positions, which corresponds to measured weather conditions. Additionally, tensiometer values indicate that, in early season of 2013 in 50 cm depth soil was wetter than in early season of 2012, which also corresponds to the finding that weather in early 2012 was hotter and drier.

Like for tensiometer measurements of 2012 also TDR values of CT showed the lowest soil moisture content in 0 to 30 cm depth throughout most of the season. But TDR probe results partly differed from tensiometers for NT and ET. One reason for this inhomogeneity could be the above mentioned problem of using drip irrigation systems and the positioning of the single sensors. In addition, tensiometers measured soil moisture tension in 25 cm depth, while TDR probes measured soil moisture content from 0 to 30 cm depth. For 30 to 60 cm depth, results correspond well to tensiometer values in 50 cm depth. Overall, although some differences between TDR and tensiometer results were visible, the main overall picture is similar, especially in the deeper soil layers. Inconsistencies might be explained by differences in measurement positions, in depths and in spatial distribution, and through the use of drippers and thus inhomogeneous soil wetting patterns. Like for tensiometer measurements, precipitation and irrigation events have been detectable in TDR measurements. TDR probe measurements are supposed to continuously function, but many of the installed sensors failed. Thus the system seems to be not very suitable to the prevailing conditions of the orchard. TDR sensors have not been widely accepted due to installation and soil disturbance difficulties (EVETT et al., 2012). The TDR measurement technique is mainly used in sandy soils, and possibly it is more suitable for sandy soils and not for the heavy soil of this experimental orchard.

Diviner 2000 measurements have a higher soil depth resolution than the other used sensors, and some interesting results were obtained. No significant change in soil moisture below 90 cm depth has been recorded during the whole measurement time. Trees were planted in autumn of 2011 and the main part of the roots is supposed to be well above 90 cm. Overall, a similar main course for each treatment in several depths down to 80 cm is visible. Highest changes occurred in the uppermost 30 cm, with changes of up to 22 %, 18 %, and 15 % Vol. soil water content in 10 cm, 20 cm, and 30 cm depth, respectively. A clear effect of irrigation has been visible from 20 to 60 cm depth in 2012 and in 2013, which generally corresponds to findings of tensiometer and TDR measurements. In general, changes were less, the deeper the measurement. Diviner 2000 measurements are moderately sensitive to temperature changes and accuracy changes with soil moisture. Additionally, only small volumes of soil near the access tube are measured, which makes measurements sensitive to small scale variations in soil water content close to the access tube (EVETT et al., 2006), but air pockets beside the access tube can lead to errors.

Overall, all used soil moisture measurement systems showed advantages as well as disadvantages. By comparing the different systems, a medium to good agreement in between the results was obtained. Some discrepancies may have been caused by the above described different measurement positions and by dissimilar measurement techniques and depths and shows that the positioning in the orchard is very important for the growers. A disadvantage of the systems is that only the available soil water at the particular measurement position is measured and not necessarily how much water is available to the plant. Therefore, a direct measurement of plant water status should be advantageous to any soil moisture measurements. All used soil moisture measurement systems were easy to use, and, except for the failure of the TDR probes, reliable. TDR and tensiometer sensors were not very labor intensive while Diviner 2000 measurements are labor intensive and do not provide continuous measurements. Rain events as well as irrigation events were detectable with all three measurement techniques, although the time-resolution of the continuous TDR and tensiometer measurements was much better than of the only weekly performed Diviner 2000 measurements. This also led to lower visibility of single rain and irrigation events of the Diviner 2000 measurement system. On the point of practical implication continuously recording soil moisture measurements with low labor needs, e.g. tensiometers, are clearly recommended.

6.3.7 Use of additional irrigation in Germany

Obtained experimental results indicated that the use of irrigation in newly planted apple orchards in Germany can be very beneficial. Although results of first yield in 2013 did not imply much higher first yields in irrigated compared to non-irrigated apple trees, tree size and establishment has been improved by irrigation. 2013 was a wet year and thus no huge effect of additional irrigation was expected and visible, but beneficial effects of 2012 were still detectable and significant between treatments in 2013. The presented results of the field experiments have shown that additional irrigation can lead to faster growth and establishment of young apple trees. Excessive vegetative growth in mature apple orchards is undesirable, because it leads to higher pruning costs and shaded fruits, but for the first years it is very helpful for a fast tree development. Furthermore, additional irrigation may ensure tree survival in hot and dry years like for example 2011 in Germany. In the current study a clearly improved growth in 2012 was achieved through irrigation which still was statistically significant in 2013, although 2013 was a wetter year than 2012 and both years were wetter than the average. But results also indicate that for German growers it remains a very difficult decision, because economic benefit and usefulness highly depend on weather conditions during the particular years and soil water resources. But since effects were already very beneficial even under the wetter than usual conditions in respect to the projections for the future climate in Germany irrigation is clearly recommended for new orchards.

For a final decision also economic considerations have to be taken into account. In addition, it is also not only the question whether additional irrigation shall be used or not, but also which irrigation system is the best to use. In the presented case ET used less water than NT in both years, with similar positive effects. Using an ET based irrigation can help to safe water, but it also needs more data and calculations and therefore might not be used by growers. The major advantage of drip irrigation systems is that they use less water than sprinkler systems while maintaining fruit yield and quality (FALLAHI et al., 2010; FALLAHI et al., 2013). Overhead sprinkler systems have the advantage that they can be additionally used for frost protection. In common with the presented results TOJNKO & CMELIK (2004) also found positive effects of irrigation on tree performance of apple orchards in Slovenia. In many apple growing regions around the world it is already standard to use irrigation systems. Especially in modern high density orchards rapid vegetative growth is needed during the first years after planting in order to build up the tree size and thereby prepare the tree for early production (TOJNKO & CMELIK, 2004). In addition, also for mature orchards an installed irrigation system ensures high production during very dry years.

7 DEVELOPMENT OF A WATER SUBMODEL FOR MALUSIM

7.1 Introduction

One of the disadvantages of MaluSim is that it does not consider any water status of apple trees and this surely is one of the future main topics in worldwide apple production. In the past, many different experiments concerning irrigation and water deficit effects in apple orchards have been conducted, but the previously acquired knowledge has not been widely connected. Therefore the attempt has been made to integrate a water submodel in MaluSim, which is based on findings of published literature. The idea behind the submodel is on the one hand to improve the original model and on the other hand to expand its possible areas of use, since effects of additional irrigation and water deficits become more and more important with the worldwide Climate Change (STÖCKLE et al., 2011).

7.2 Water submodel development

In the following the development process of the water submodel is described, including a description of the main principles it is based on. All introduced relationships were based on findings in the literature. Parts of the water submodel have been developed in cooperation with Alan Lakso, the developer of the original MaluSim model. At the beginning, it had to be checked which parts of the model are supposed to be affected by tree water status. After analyzing MaluSim, four main parts were found: long shoot and spur growth, photosynthesis, respiration rates, and fruit growth. For these parts, the available information in published literature has been collected and the software STELLA® has been used to include new parts into the MaluSim model. In general, new effects were added at first by including the found relationship (equation) and then connecting the new parameter to existing parameter (existing parameter then are affected by the new ones).

A comprehensive model would model the water stress in the tree as well as the effect of the water stress on the growth and gas exchange. However, such a comprehensive model is beyond the scope of this thesis. Also, measurement of soil water status was not found in this study to be a good predictor of tree water stress. Therefore, the research and modeling work focused on the effects of water stress on tree growth and gas exchange.

7.2.1 General water submodel input

At first, a plant water status indicator had to be selected to be able to link water deficit effects to the existing relationships and parameter of the model. Midday stem water potential was chosen as the plant water status indicator because it is supposed to be a better stress indicator for processes, like photosynthesis, which also occur at daytime, than for example predawn water potential. Midday stem water potential has been reported to be a reliable water status indicator in apple and other fruit tree crops (NAOR et al., 1995; SHACKEL et al., 2000; DOLTRA et al., 2007; VAN LEEUWEN et al., 2009; RUIZ-SÁNCHEZ et al., 2010). Midday stem water potential (WatPot MD) has been included into the MaluSim framework as a function of days, and it is an input parameter inserted by the user. This water status indicator then has been connected to the parts of the model, which are supposed to be affected by a change in tree water status.

7.2.2 Long shoots and spurs

MaluSim calculates the fraction of growing shoots and spurs, which is a function of accumulated degree days. This fraction of growing shoots and spurs is then used to calculate leaf area. Therefore, a change in fraction of growing shoots or fraction of growing spurs also leads to a change in total leaf area. The hypothesis for long shoots and spurs, and thus leaf area development, was, that under water deficit, shoot growth is reduced and stops earlier. An effect of additional irrigation or water deficit on shoot growth has been reported by several authors (MAGGS, 1961; POWELL, 1976; DAVIES & LAKSO, 1979; LANDSBERG & JONES, 1981; LAKSO, 1985; FORSHEY & ELFVING, 1989; BUWALDA & LENZ, 1992; EBEL et al., 1995; AL-HAZMI, 1996; KILILI et al., 1996b; MILLS et al., 1996; O'CONNELL & GOODWIN, 2007; TALLUTO et al., 2008; LO BIANCO et al., 2012). E.g., BUWALDA and LENZ (1992) found that a reduction of water supply to 50 and 25 % reduced total dry weight of the trees to 58 and 33 %, respectively. Additionally, leaf area has been reduced from 6.2 m^2, to 2.8, and 1.4 m^2, while the reduction in shoot dry weight was from 2162 g/tree, to 1210 g, and 626 g, respectively.

In general, soil moisture stress is known to reduce shoot growth, while irrigation is thought to increase it (MAGGS, 1961; FORSHEY & ELFVING, 1989). Only very few data is available on the relationship between Ψ_{stem} and shoot growth. Differences between reported values in the literature might be due to differences in weather conditions (temperature, VPD), measurement technique, or possibly caused by an osmotic adjustment of trees. The relationship used in the water submodel (Figure 18) is mainly based on data of EBEL et al. (1995), AL-HAZMI (1996), O'CONNELL and GOODWIN (2007), and on unpublished data of Alan Lakso.

If water stress occurs, the fraction of growing shoots is reduced and the amount of growth is less. For this reason a water stress effect on shoot and spur growth (WtrStrEffShGr) based on midday stem water potential (WatPot MD), according to Figure 18, has been added to the MaluSim model. This leads to a reduction of growing shoots and spurs if water potential is equal or lower than -1.1 MPa. Above this value no reduction occurs. A water potential of -1.5 MPa leads to a reduction down to 75 %. If midday water potential reaches values of -2.6 MPa and lower, no shoot and spur growth is supposed to occur.

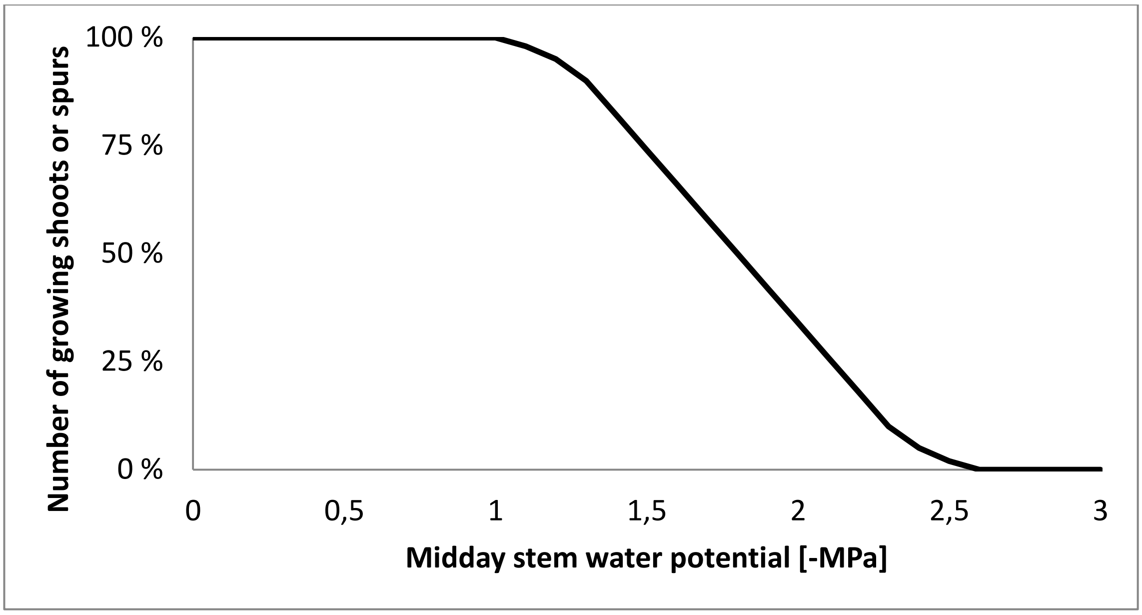

Figure 18: Relationship between midday stem water potential and number of growing shoots or spurs used in the water submodel.

Due to the small database the set threshold and the used relationship might change during the further development of the water submodel. In the current case the effect starts at a similar point as the effect on photosynthesis, but not at the exact same point. This difference allows to detect the water deficit effects on the single submodels in the simulation runs, and also to be able to check that all described effects are properly included in the model framework.

7.2.3 Photosynthesis

It is widely known that water deficit affects photosynthesis of plants (see Chapter 2.4.2). NAOR (1998) found a relationship between stem water potential and stomatal conductance for apple trees. In addition, a relationship between leaf photosynthesis and stomatal conductance was found by WÜNSCHE et al. (2000). The daily gross photosynthesis (g CO_2 day^{-1}) per tree calculation in MaluSim is based on the integral model described by CHARLES-EDWARDS (1982). Main photosynthetic parameter used for calculation are maximum light saturated photosynthetic rate (P_{max}) and photochemical efficiency (PChemEff). The only available published data about a relationship between midday stem water potential and maximum net photosynthetic rate has been measured in a single potted apple tree (STEPPE et al., 2008; DE SWAEF et al., 2009). No data about changes in photochemical efficiency under water deficits was available in the literature. The results of light response curves in Figure 16 indicate little or no difference in the initial slope of the light response curves for different water status. For this reason no effect of water status on photochemical efficiency has been included into MaluSim, at this point.

The relationship between midday stem water potential and P_{max} (Figure 19) is based on the published data of STEPPE et al. (2008) and DE SWAEF et al. (2009) for potted apples. The relationship has been included into MaluSim by using a water stress effect on P_{max} (WtrStrEffPmax), which is based on midday stem water potential (WatPot MD). P_{max} is supposed to be not affected when midday stem water potential is between 0 and -0.99 MPa. Starting from -1 MPa P_{max} is reduced, with values below -2.9 MPa leading to a total stop of photosynthesis.

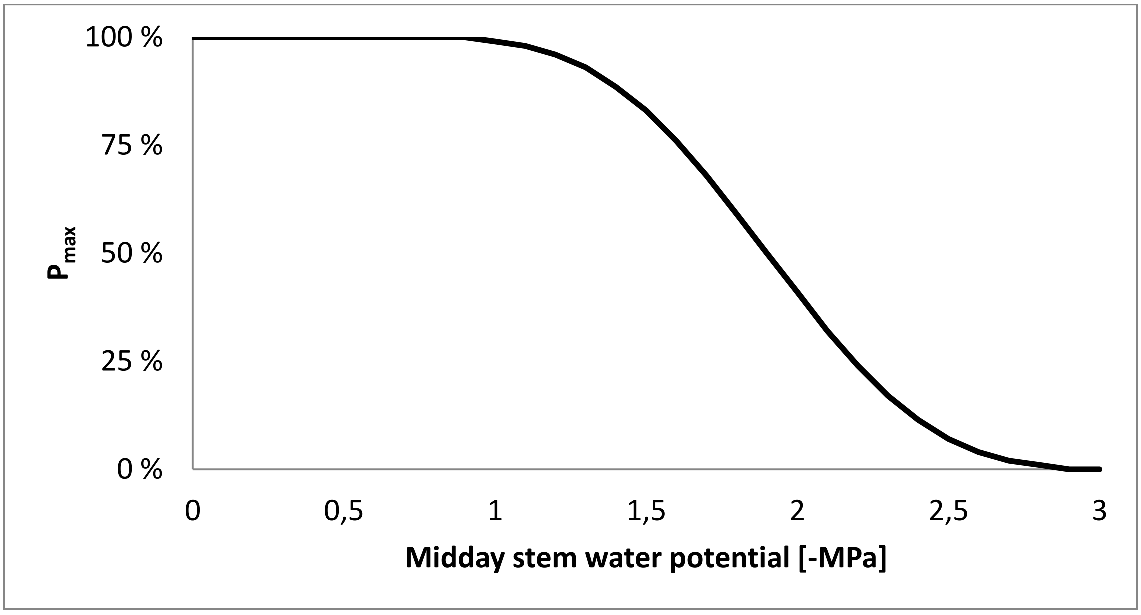

Figure 19: Relationship between midday stem water potential and Pmax used in the water submodel, based on published data of STEPPE et al. (2008) and DE SWAEF et al. (2009) for potted apples. (y= -0.0107+1.0190/(1+exp(-(x-1.9018)/-0.2537))).

Osmotic adjustment has been found to be significant in apple (GOODE & HIGGS, 1973; LAKSO, 1979; LAKSO et al., 1984). Osmotic adjustment is not included in the water submodel, but would result in a shift of the curve into a more negative section, while the general shape of the response is likely similar. A possible way, to include osmotic adjustment, would be to use a function of cumulative midday stem water potential however, such data is rare. Osmotic adjustment in apple trees is still not fully understood and too few data are available to be able to include it into the model at the moment.

7.2.4 Respiration rates

Data about water deficit effects on respiration rates is very rare and partly contradictory. PSARRAS and MERWIN (2000) found that root respiration rates increased with soil moisture stress. HSIAO (1973) also reported various results for effects of water stress on respiration, but overall concluded that respiration rates are generally suppressed by moderate to severe stress. Differences in experimental results are likely to be caused by differences in stress development and severity. Often a very short increase in respiration rates after water stress induction has been found, followed by a clear decrease. For apple, respiration rates of whole plants (WIBBE & BLANKE, 1997), leaves (JONES & FANJUL, 1983), and root systems (LOMBARDINI et al., 2001) have been found to decrease under medium to severe stress.

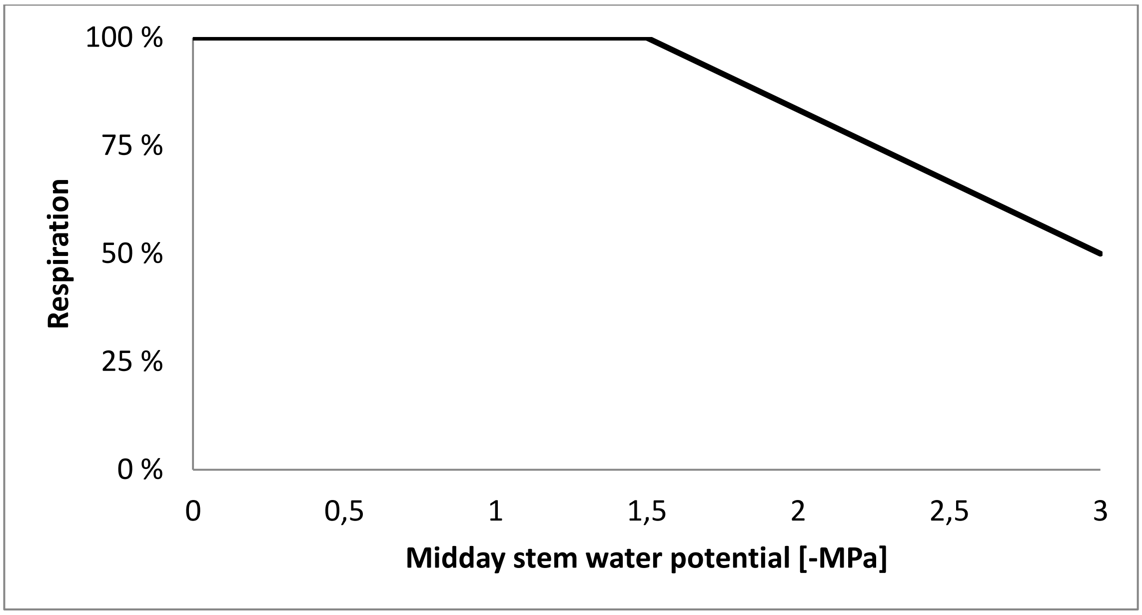

Figure 20: Relationship between midday stem water potential and respiration rates of plant organs used in the water submodel.

According to the available literature for apple, a relationship for respiration rates of fruits, wood and leaves has been included into the water submodel (Figure 20). For this a water stress effect on respiration (WtrStrEffResp) has been used. Respiration rate is regulated to be unaffected by midday stem water potentials of 0 to -1.5 MPa. Below -1.5 MPa a linear decrease of respiration rate is expected to occur with a 50% reduction at -3 MPa.

7.2.5 Fruit growth and other current limitations

Although effects of water deficits on fruit growth have been reported in the literature (NAOR et al., 1997; ATKINSON et al., 1998; EBEL et al., 2001; NAOR et al., 2008; NASCHITZ et al., 2010; GARCÍA PETILLO et al., 2011), no direct effect of water deficit on fruit growth has been included into the submodel for now, to avoid a double effect. Fruit growth rate is already decreased through decreases in photosynthesis and active leaf area and thus by the decreased assimilates which are available for fruit growth. In case this should not be sufficient an additional effect has to be included. For this reason the submodel has to be tested and compared with experimental data without using a fruit growth reduction component, at first. After some tests it should become clear if an additional direct effect on maximum fruit growth has to be included and how strong the effect has to be. Besides direct fruit growth effects also trunk and root growth effects have not been considered for the same reasons. Additionally, it is unclear if water status of the tree also changes the carbon allocation pattern itself, or only changes the amount of carbon, which is available for partitioning. The study of BUWALDA and LENZ (1992) indicate that mild water stress does not affect the carbon partitioning pattern much, while severe stress changes the allocation pattern of the tree.

7.2.6 Schematic view of the new water submodel

An overview of the connections of the new water submodel to the already existing original submodels is shown in Figure 21.

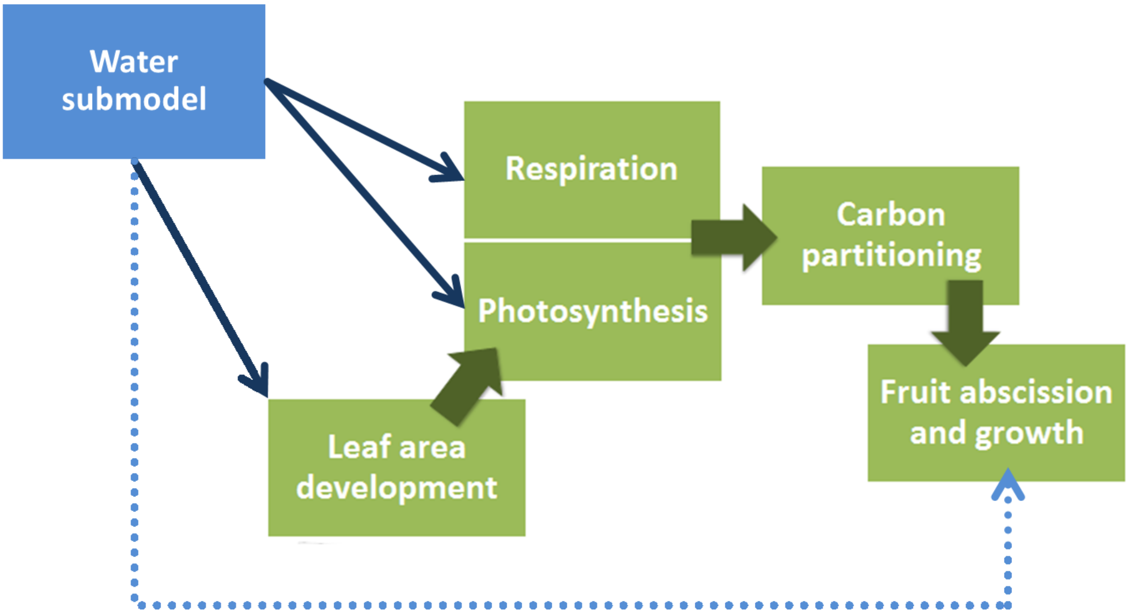

Figure 21: Schematic diagram of the interactions of the new water submodel (blue) with the five original submodels of MaluSim (green), with dark blue bold arrows showing direct effects and the light blue dotted arrow an indirect effect.

The fruit growth and abscission submodel is only indirectly affected by the water submodel through effects on leaf area development and on respiration and photosynthesis.

7.3 Simulation runs

7.3.1 Description of simulation runs

Although no experimental field data of established orchards was available for comparisons, test simulation runs of the new water submodel were conducted for the location Zornheim. The modified model 'G4-4' (fruit submodel modification) that obtained best results (see Chapter 5) was used as a basis and parameter were set as described in 5.1.2. Tests using whole season fixed midday stem water potentials were conducted for -0 MPa (G4-4 WatPot0), -1 MPa (G4-4 WatPot1), -1.5 MPa (G4-4 WatPot1.5), -2 MPa (G4-4 WatPot2), -2.5 MPa (G4-4 WatPot2.5), and -3 MPa (G4-4 WatPot3), and using input data for the location Zornheim. In addition, simulation runs with an early (from budbreak to two weeks after full bloom) medium water deficit and a late (from fruit 30 mm stage (mid-season) to end of simulation) medium water deficit, as well as with an early severe water deficit and a late severe water deficit were conducted (see Table 19).

Table 19: Test simulation runs with early and late water deficits, with early occurring deficits of -1.5 MPa (G4-4 ED1.5 Day0-50) and of -2 MPa (G4-4 ED2 Day0-50) from DABB 0 to 50, and with late occurring deficits of -1.5 MPa (G4-4 LD1.5 Day71-98) and of -2 MPa (G4-4 LD2 Day71-98) from DABB 71 to 98.

	G4-4 ED1.5 Day0-50	**G4-4 LD1.5 Day71-98**	**G4-4 ED2 Day0-50**	**G4-4 LD2 Day71-98**
Water potential of -0 MPa	from day 51 to 98	from day 0 to 70	from day 51 to 98	from day 0 to 70
Water potential of -1.5 MPa	from day 0 to 50	from day 71 to 98	-	-
Water potential of -2 MPa	-	-	from day 0 to 50	from day 71 to 98
Input of	Zornheim	Zornheim	Zornheim	Zornheim

7.3.2 Results of water submodel test simulation runs

Simulation runs using the new water submodel with fixed seasonal midday stem water potentials showed calculated final fruit numbers between 0 and 237 (Table 20). A water potential of -0 MPa led to the maximum number of final fruits of 237, which equals to the simulated fruit number of the model 'G4-4' in chapter 5. Compared to this, the calculated final fruit number was slightly reduced for a simulation run with a seasonal midday stem water potential of -1 MPa. Using a water potential of -1.5 MPa showed a reduction of final fruit number to only half of the one using -1 MPa. Water potentials of -2 MPa and lower led to a calculated drop of all fruits.

Table 20: Final fruit numbers calculated by MaluSim for fixed seasonal midday stem water potentials of -0 MPa (WatPot0), -1 MPa (WatPot1), -1.5 MPa (WatPot1.5), -2 MPa (WatPot2), -2.5 MPa (WatPot2.5), and -3 MPa (WatPot3) using model 'G4-4'.

	WatPot0	WatPot1	WatPot1.5	WatPot2	WatPot2.5	WatPot3
# fruits	237	234	112	0	0	0

Simulation runs with medium and severe early water deficits ('ED1.5 Day0-50' and 'ED2 Day0-50') led to reduced final fruit numbers of 130 and 0 fruits, respectively. While for a late deficit fruit numbers were not affected for medium ('LD1.5 Day71-98') and slightly reduced for severe water deficit ('LD2 Day71-98') (see Table 21).

Table 21: Final fruit numbers calculated by MaluSim ('G4-4') for test simulation runs with early and late water deficits, with early occurring deficits of -1.5 MPa (ED1.5 Day0-50) and of -2 MPa (ED2 Day0-50) from DABB 0 to 50, and with late occurring deficits of -1.5 MPa (LD1.5 Day71-98) and of -2 MPa (LD2 Day71-98) from DABB 71 to 98.

	ED1.5 Day0-50	LD1.5 Day71-98	ED2 Day0-50	LD2 Day71-98
# fruits	130	237	0	223

Besides final fruit number, additionally daily canopy photosynthesis differed for water submodel simulation runs (Figure 22). Highest daily canopy photosynthesis has been calculated for 'WatPot0' and 'WatPot1'. Lowest values, close to zero during the whole season, were simulated for water potentials below -2.5 MPa ('WatPot2.5' and 'WatPot3'). 'WatPot1.5' and 'WatPot2' show an intermediate course of daily canopy photosynthesis.

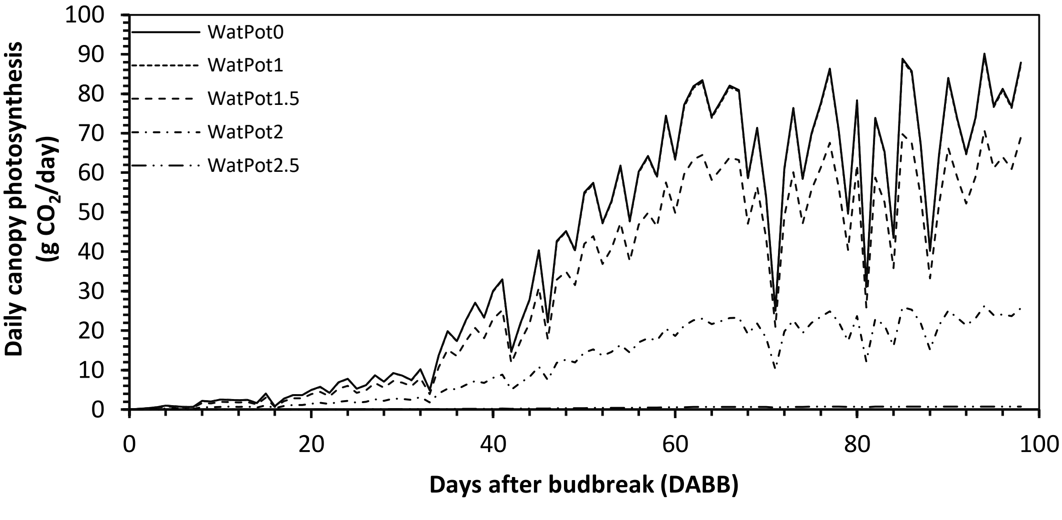

Figure 22: Calculated daily canopy photosynthesis of test simulation runs with fixed seasonal midday stem water potentials of -0 MPa (WatPot0), -1 MPa (WatPot1, highly similar to WatPot0)), -1.5 MPa (WatPot1.5), -2 MPa (WatPot2), and -2.5 MPa (WatPot2.5). The fixed seasonal midday stem water potential of -3 MPa led to a calculated seasonal canopy photosynthesis of zero.

Compared to 'WatPot0' calculated canopy photosynthesis on DABB 98 was reduced to 99.5 % for 'WatPot1', to 78.5 % for 'WatPot1.5', to 29.3 % for 'WatPot2', to 0.9 % for 'WatPot2,5', and to 0 % for 'WatPot3'.

For simulation runs of late seasonal water deficits no differences compared to 'WatPot0' can be seen during the early season, and only slight reductions are calculated in the late season (Figure 23). Compared to this, early deficits, in particular for 'ED2 Day0-50', led to clearly visible lower daily canopy photosynthesis in the early season. Compared to 'WatPot0', daily canopy photosynthesis on DABB 50 was reduced to 76.2 % for an early deficit of -1.5 MPa ('ED1.5 Day 0-50'), and to 26.2 % for an early deficit of -2 MPa ('ED2 Day 0-50'), while the late deficit simulations had 100 % ('LD1.5 Day71-98' and 'LD2 Day 71-98'). On DABB 98, daily canopy photosynthesis was still reduced to 92.0 % for 'ED1.5 Day 0-50', and to 89.0 % for 'ED2 Day 0-50'. When comparing the late deficit simulations to 'WatPot0' daily canopy photosynthesis on DABB 98 was reduced to 89.3 % for 'LD1.5 Day71-98' and to 56.3 % for 'LD2 Day 71-98'.

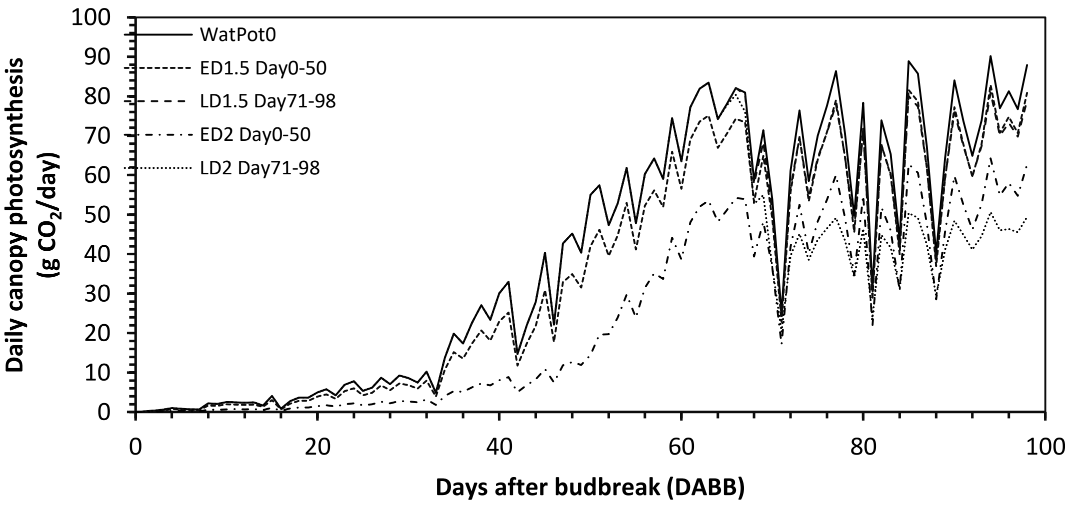

Figure 23: Calculated daily canopy photosynthesis of test simulation runs with early and late water deficits, with early occurring deficits of -1.5 MPa (ED1.5 Day0-50) and of -2 MPa (ED2 Day0-50) from DABB 0 to 50, and with late occurring deficits of -1.5 MPa (LD1.5 Day71-98) and of -2 MPa (LD2 Day71-98) from DABB 71 to 98.

Calculated active leaf area of 'WatPot0' and 'WatPot1' is equal during the whole season (Figure 24). While 'WatPot1.5' and 'WatPot2' show intermediate behavior, 'WatPot2.5' and 'WatPot3' have the lowest values of below 0.5 m^2 from DABB 0 to 98 (calculated active leaf area for 'WatPot3' is 0). Final active leaf area on day 98 is 5.5 m^2 for 'WatPot0' and 'WatPot1', which equals a LAI of 1.6.

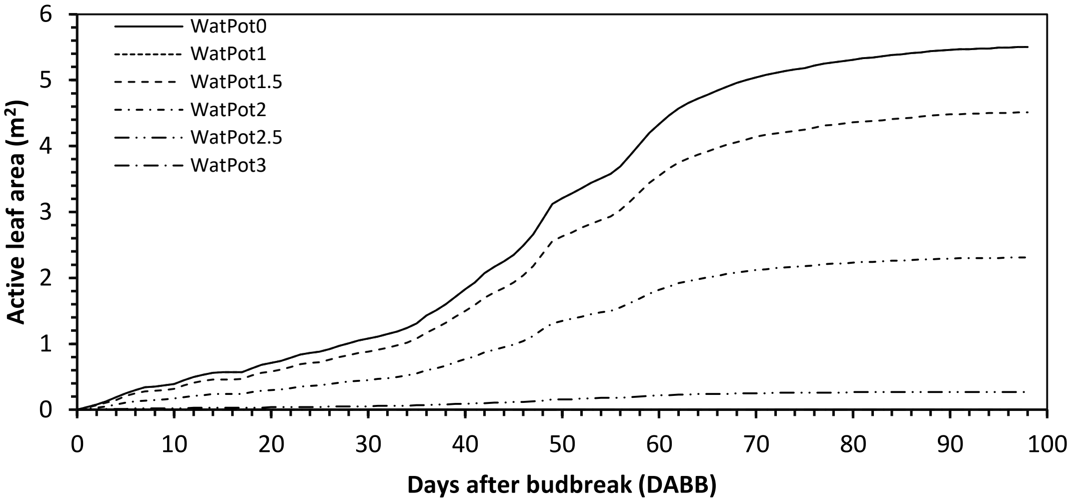

Figure 24: Calculated active leaf area per tree (m^2) development of test simulation runs with fixed seasonal midday stem water potentials of -0 MPa (WatPot0), -1 MPa (WatPot1; equals exactly to course of WatPot0), -1.5 MPa (WatPot1.5), -2 MPa (WatPot2), -2.5 MPa (WatPot2.5), and -3 MPa (WatPot3; equals 0 during the whole simulation period).

For simulation runs of late season deficits, active leaf area of both late deficit tests reach an active leaf area of over 5 m^2 (Figure 25). Early deficit simulations lead to lower values of maximum active leaf area, of 4.8 and 3.5 m^2, for 'ED1.5 Day0-50' and 'ED2 Day0-50', respectively.

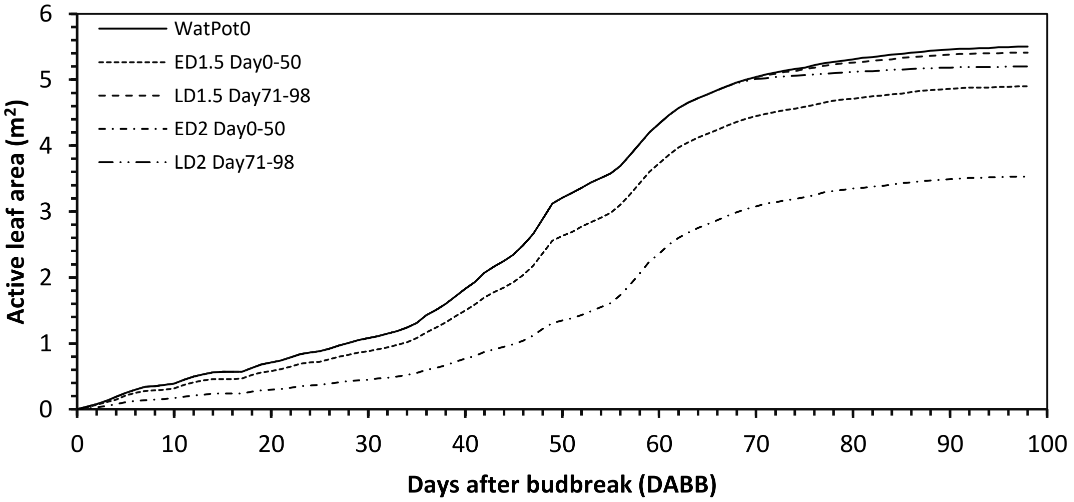

Figure 25: Calculated active leaf area (m^2) development of test simulation runs with early and late water deficits, with early occurring deficits of -1.5 MPa (ED1.5 Day0-50) and of -2 MPa (ED2 Day0-50) from DABB 0 to 50, and with late occurring deficits of -1.5 MPa (LD1.5 Day71-98) and of -2 MPa (LD2 Day71-98) from DABB 71 to 98.

In general, seasonal active leaf area shows similar reductions with lower water potentials as daily canopy photosynthesis, but for daily canopy photosynthesis reductions are more profound, caused by the combination of the active leaf area effect and the Pmax effect.

7.4 Discussion

In the scope of this thesis it was possible to include a water submodel into MaluSim by using published data and relationships. The submodel is based on water deficit effects, included by midday stem water potentials, on calculated physiological processes of the model. First simulation runs of the model indicate a realistic behavior and simulated various effects of different water deficit levels and periods on number of fruits, on daily canopy photosynthesis, and on active leaf area development.

Overall, water relations of apple trees are extremely complex and dynamic. Many different factors (temporal, atmospheric, structural, physiological, and cultural ones) may have an effect on the response of apple trees to a particular water status. JONES and TARDIEU (1998) summed up some of the most important theoretical points about water relations modeling. They concluded that models work best in homogeneous systems (JONES & TARDIEU, 1998), but apple canopies and apple root systems are very heterogeneous. Non-uniform root distribution and heterogeneity of soil can make soil water measurements useless for field tree water models. Low root density and the clumping of apple roots (LAKSO, 2003) additionally complicates the modeling of soil water status, which itself is already known to be difficult (JONES & TARDIEU, 1998). Apple orchard water use varies with tree characteristics, training systems and climate. This constrains an easy and exact development of models. The heterogeneity of apple orchards adds some complexity to the modeling approach and increases the attainable modeling error. A further difficulty in apple tree water relations modeling is that rainfall interception by canopies may be an important component of orchard water balance, but little knowledge about this is available (CALHEIROS DE MIRANDA & BUTLER, 1986).

One of the main points of the water submodel is the use of midday stem water potential as a water status indicator. Plant based measurements are very promising for detecting drought stress, but strongly depend on microclimate. They have the advantage of measuring the plant’s response to the prevailing environmental conditions, but often finding usable thresholds is difficult. Ψ_{stem} is a reliable and robust direct indicator of plant water status (SHACKEL et al., 2000; NAOR, 2008). A limitation of Ψ_{stem} is that it is labor intensive and a destructive measurement. Ψ_{stem} has been proposed and used by some researchers as a reliable tool for irrigation scheduling (BEGG & TURNER, 1970; MCCUTCHAN & SHACKEL, 1992; SHACKEL et al., 1997; NAOR & COHEN, 2003; INTRIGLIOLO & CASTEL, 2004; DOLTRA et al., 2007), but such a measurement is usually not conducted by growers and cannot be automated. For this reason a further improvement of the water submodel would be the calculation of Ψ_{stem} from other easier available inputs, like for example soil moisture measurements, which is an often measured parameter in commercial orchards. In some apple field experiments, Ψ_{stem} has been measured but often relationships to other parameter like for example soil water content have not been considered (e.g. NAOR, 2000; LOMBARDINI et al., 2004; GIRONA et al., 2010; GARCÍA PETILLO et al., 2011; GONZÁLEZ-TALICE et al., 2012). EBEL et al. (2001) found a nonlinear relationship between plant water potential and total available soil water for their experimental data. No easy single relationship between soil moisture measurements and stem water potential has been found in the conducted field experiment in Geisenheim (see Appendix Figure 41 to Figure 44). Possibly obtained stem water potentials and soil drying did not reach sufficient levels. Soil moisture related measurement techniques also have the disadvantage that root systems and by roots exploited soil volumes differ significantly between cultivars, soil types, and used irrigation systems. Therefore, although Ψ_{stem} measurement also does have many disadvantages, it is still the best available method for water status determination at the moment.

Although many field experiments concerning water stress of apple trees have been conducted in the last years, it is very difficult to get all needed data to test the water submodel by using data of other researchers. Therefore, an external validation of the new submodel has not been possible. For this aim, it is necessary in future to measure all relevant parameter in the same field experiment. Furthermore the development of the above indicated ‘soil part’ is also very desirable. An alternative to the inclusion of a ‘soil part’ is the development of new sensors for water status detection in trees. Some promising ideas for this possibility emerged in the last years (e.g. PAGAY et al., 2014), but are not yet available at the moment. For the further development and validation of the MaluSim water submodel, further research is necessary but first test simulation runs are promising and indicate a general realistically behavior.

Some models have been developed to model water uptake of apple trees (GREEN & CLOTHIER, 1999; GONG et al., 2006), but do not model stem water potential of apple trees and therefore are not very comparable. For a review about water uptake and water use models the reader is referred to GREEN et al. (2006) or JONES (2014b). Water status has also been included in models for other fruit tree crops. DA SILVA et al. (2011) even calculated stem water potentials for peach trees. But although they reported reasonable results, values have not been directly validated; only checked for plausibility. MARSAL and STÖCKLE (2012) used the model ‘CropSyst’ to simulate Ψ_{stem} of apple, pear, and peach trees. They compared the simulated values with data obtained in the field with medium to good success (MARSAL & STÖCKLE, 2012; MARSAL et al., 2014), but water potential values were mainly above -1.2 MPa and thus in a non-water stress condition. Simulations of 'CropSyst' are thought to be used to support regulated deficit irrigation scheduling. Also, the model is not able to calculate carbon balance of trees or fruit abscission. ZWEIFEL et al. (2001) and STEPPE et al. (2006) modeled the dynamics of stem water potentials based on continuously measured variables on the plant itself or in its microenvironment. STEPPE et al. (2008) extended this approach to calculate irrigation needs of trees. By measuring sap flow they were able to calculate stem water potentials of unstressed trees, but the model failed under stress conditions. Anyway, it might be possible to use sap flow measurements as a model input to correctly calculate stem water potentials or general water status of apple trees even under stress conditions and this should be further investigated. But sap flow measurements also have some disadvantages and at the current state it seems not very likely that they will be highly used by growers. For now, the modeling of tree water consumption is not practical due to our inability to supply the proper inputs for the models (NAOR, 2008).

Overall, more particular research regarding the relationship between Ψ_{stem} and its influencing parameter is needed before this parameter can be calculated by MaluSim. Another idea, instead of using soil moisture measurements, is to use a water balance concept, where soil water status is calculated. Problems associated with this approach are differences in soil, unclearness in terms of effective rainfall events, uncertainties in calculation of soil water content and evapotranspiration, and little knowledge about root distribution and rooting depth. Although drafts of the soil water part exist in the water submodel, at first the plant part of the water submodel has to be validated. Including too many new data into MaluSim should be avoided to still be able to test every new inclusion for necessity and reliability. For now, Ψ_{stem} appears to be the most suitable water stress indicator for the water submodel approach, but the development of new plant water status sensors might also lead to other useful inputs. After the validation is completed, a next step to further improve the water submodel can be to add a soil water uptake component or another component to calculate water deficits.

Test simulation runs of MaluSim using the water submodel showed that without including a direct water stress effect on fruit development, the model already calculated some strong effects of water stress on fruit abscission. This indicates that the indirect effect might be sufficient but a validation is needed. The included water submodel generally shows a realistic behavior in the first tests. No evidence for a wrong integration of the relationships is visible in the simulation run using a water potential of 0 MPa, which shows the same outputs as 'G4-4' without a water submodel.

Simulated daily canopy photosynthesis showed a higher reduction at the same water potential value than the simulated reduction of active leaf area. This effect is caused by the included direct effect of water potential on photosynthesis in combination with the indirect effect of a reduction of active leaf area, due to reduced shoot growth. When having a closer look at the simulation runs that use a water potential of -1 MPa it becomes clear that the MaluSim model calculated that photosynthesis is already slightly affected, while the threshold for active leaf area reduction is -1.1 MPa and thus it is not reduced. This shows that the described on literature data based functions (thresholds) were properly included into the MaluSim model framework. The thresholds (and functions) might still change through the further development and testing of the water submodel.

It is known that shoot growth is one of the first processes affected by water deficits (LAKSO, 2003), which is probably caused through the fact that shoot growth mainly takes place during the afternoon (POWELL, 1976). In the current water submodel, photosynthesis is thought to be the first process that is affected by water deficits. This is based on the published data of STEPPE et al. (2008) and DE SWAEF et al. (2009) for potted apples. In addition, it is not helpful to add two different effects (the one on photosynthesis and the one on shoot growth) at the exact same threshold. In this case it is not possible to understand and differentiate the simulation results. But the experimental results of this thesis and the found relationship between Ψ_{stem} and photosynthesis indicate that a lower threshold should be used in the water submodel.

While mature apple leaves are thought to be able to adjust osmotically, this has not been found for shoot tips and shoot growth (LAKSO et al., 1984). It is thought that when apple leaves osmotically adjust, the found relationship between photosynthesis and midday stem water potential generally stays similar, but shifts to more negative midday stem water potentials. But osmotic adjustment has not been included into the MaluSim water submodel yet. Osmotic adjustment is also suggested to occur in fruit and roots (WANG et al., 1995). Shoot growth is thought to be more sensitive to water deficit than fruit growth (FORSHEY & ELFVING, 1989; EBEL et al., 1995; FALLAHI et al., 2010). Fruit growth rate was found to start decreasing with midday stem water potentials lower than -1.3 MPa (NAOR et al., 1997).

Test simulation runs using an early and a late water deficit additionally indicate that an early deficit in any case strongly affects tree development and numbers of fruits, while a later water deficit after fruit set and much shoot growth usually is less severe on fruit numbers and leaf area. This has also been found in experimental results using early and late deficit treatments (POWELL, 1974; KILILI et al., 1996a; MILLS et al., 1996). The simulation run also indicates that for late water deficits, leaf area development is nearly completed and therefore only slight reductions of active leaf area occur. Leaf area of a late deficit treatment has not been significantly different to a fully irrigated control treatment in 'Braeburn' (MILLS et al., 1996).

Overall, although the MaluSim water submodel should be externally validated in future, test simulation runs appear to give realistic outputs. Additionally, through the work on the water submodel, it was possible to identify the most important factors that have to be considered for apple tree water relations modeling in respect to carbon balance. Although the water submodel cannot be used for irrigation purposes at the moment, it can already be used for theoretical simulation runs concerning water deficit effects.

8 GENERAL DISCUSSION AND CONCLUDING REMARKS

This study showed that modelling can be a very useful tool to enhance the comprehensive understanding of complex biological systems like apple trees, its physiological processes and its influencing parameters. In the scope of this thesis it was possible to adapt a current model for apple trees, which can be used in Germany and Central-Europe to address the major problems of commercial apple production. Beside the parameterization it was possible to successfully modify the fruit submodel to compare calculated to measured final fruit numbers, and to integrate a theoretical water submodel. In the past, no comparable model existed for Central-Europe.

This work provides some potentially useful additions to the MaluSim model itself and its possible area of usage has been extended. Not only to Germany or Central-Europe, but also to problems related to fruit abscission and water status. Comparisons of real to calculated final fruit numbers show promise that it can become possible to model fruit abscission and use the fruit submodel, although the fruit growth and abscission itself still has to be validated against detailed field monitoring. The general relationships of MaluSim seem to be correct and it showed a realistic behavior for several different sites and regions. As already described, there exist some other models concerning apple trees, but MaluSim is probably the most comprehensive one. Although it is a process based model and only suitable for defined conditions and underlies some limitations, it has many possible uses and it can be easily parameterized for other growing regions.

The more complex model MAppleT (COSTES et al., 2008; DA SILVA et al., 2014) might be capable to address more difficult and complex questions, but is far from being validated and from providing practical applications. No other known model tries to solve the same problems as MaluSim does. Some approaches consider only single problems and try to solve them, like for example focusing only on thinning or irrigation scheduling. On the one hand to focus on one topic and fully understand it seems reasonable. But on the other hand, this study also showed that all main influencing parameters have to be considered. It is evident that only a comprehensive understanding of apple tree physiology is able to solve the main problems of today’s apple production.

Although this work also revealed some areas, where further research is highly needed and our understanding is still incomplete, it also showed that for some applications the main influencing factors are considered in MaluSim. But the model also has some limitations and cannot be used for all current fields of apple production research. Through the use of the big-fruit simplification in MaluSim it will not easily be possible to address questions like localized effects on fruit size development or internal fruit quality in future. However, it is also the question whether modelling is the appropriate approach for this or other methods like near infrared spectroscopy and other fruit quality sensors are more suitable.

The field trial provided new insights into water effects on establishing trees under temperate climate conditions. But this work also showed that our understanding of water status and water deficit effects is incomplete. The development of new plant based sensors and measurement techniques might enhance this knowledge in future. The water submodel is still on a theoretical basis, but was able to identify some areas where further research is needed. It can also already be used for theoretical studies of water deficit effects. In addition, the theoretical comparison of growing regions is able to enhance our understanding of apple productivity and influencing parameters. One interesting application for the future is the simulation of climate change effects on apple growing areas around the world. This includes finding out which regions might become suitable for commercial apple production and which ones might not be suitable anymore, or only when irrigation or frost protection is installed.

One advantage of the MaluSim model is that it can be used for theoretical and practical applications. Although future research should focus on a better understanding of fruit growth and abscission processes and its influencing factors the fruit submodel shows great promise to be integrated into practical uses. And since early season forecast of fruit abscission is impossible, theoretical modelling research can help to define a reference level of fruits which trees are capable of in most years for a particular site.

The big aim for future research is to get a comprehensive understanding of apple physiology. This will give the ability to react to and better understand changes, like climate change, new growing systems, new varieties, or new pests. One area, where research is strongly needed, involves processes, growth and other physiological mechanisms of apple roots. In addition, progress in gene expression patterns might help to solve some of the remaining uncertainties. Furthermore, the ability to collect big amounts of data with new measurement techniques is able to improve our understanding, but it also shows that modelling is likely to become even more important for future research.

9 REFERENCES

ABRUZZESE, A., MIGNANI, I., & COCUCCI, S. M. (1995). Nutritional Status in Apples and June Drop. *Journal of the American Society for Horticultural Science, 120*(1), 71-74.

AL-HAZMI, M. (1996). *Water use and physiological responses of apple trees and grapevines to water stress and cultural practices.* PhD Thesis, Cornell University, Geneva.

ALLEN, M., DEJONG, T. M., & PRUSINKIEWICZ, P. (2006). L-PEACH, an L-System Based Model for Simulation the Architecture and Carbon Partitioning of Growing Fruit Trees. *Acta Horticulturae, 707*, 71-76.

ALLEN, R. G., PEREIRA, L. S., RAES, D., & SMITH, M. (1998). Crop Evapotranspiration: Guidelines for Computing Crop Water Requirements. *FAO Irrigation and Drainage Paper, 56*.

AMÉGLIO, T., ARCHER, P., COHEN, M., VALANCOGNE, C., DAUDET, F. A., DAYAU, S., et al. (1999). Significance and limits in the use of predawn leaf water potential for tree irrigation. *Plant and Soil, 207*, 155-167.

AMTHOR, J. S. (1994). Scaling CO_2-photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research, 39*, 321-350.

AMTHOR, J. S., GOULDEN, M. L., MUNGER, J. W., & WOFSY, S. C. (1994). Testing a Mechanistic Model of Forest-canopy Mass and Energy Exchange using Eddy Correlation: Carbon Dioxide and Ozone Uptake by a Mixed Oak-Maple Stand. *Australian Journal of Plant Physiology, 21*, 623-651.

ANJUM, S. A., XIE, X.-Y., WANG, L.-C., SALEEM, M. F., MAN, C., & LEI, W. (2011). Morphological, physiological and biochemical responses of plants to drought stress. *African Journal of Agricultural Research, 6*(9), 2026-2032.

ATKIN, O. K., & TJOELKER, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science, 8*(7), 343-351.

ATKINSON, C. J., ELSE, M. A., TAYLOR, L., & DOVER, C. J. (2003). Root and stem hydraulic conductivity as determinants of growth potential in grafted trees of apple (Malus pumila Mill.). *Journal of Experimental Botany, 54*(385), 1221-1229.

ATKINSON, C. J., TAYLOR, L., TAYLOR, J. M., & LUCAS, A. S. (1998). Temperature and irrigation effects on the cropping, development and quality of 'Cox's Orange Pippin' and 'Queen Cox' apples. *Scientia Horticulturae, 75*(1-2), 59-81.

AUZMENDI, I., MATA, M., LOPEZ, G., GIRONA, J., & MARSAL, J. (2011). Intercepted radiation by apple canopy can be used as a basis for irrigation scheduling. *Agricultural Water Management, 98*(5), 886-892.

BACKES, M., & BLANKE, M. M. (2007). Water Consumption and Xylem Flux of Apple Trees. *Acta Horticulturae, 732*, 573-578.

BALANDIER, P., LACOINTE, A., LE ROUX, X., SINOQUET, H., CRUIZIAT, P., & LE DIZÈS, S. (2000). SIMWAL: A structural-functional model simulating single walnut tree growth in response to climate and pruning. *Annals of Forest Science, 57*, 571-585.

BALDOCCHI, D. D., & AMTHOR, J. S. (2001). Canopy Photosynthesis: History, Measurements, and Models *Terrestrial Global Productivity* (pp. 9-31). San Diego: Academic Press.

BANGERTH, F. (2000). Abscission and thinning of young fruit and their regulation by plant hormones and bioregulators. *Plant Growth Regulation, 31*, 43-59.

BANGERTH, F. (2004). Internal Regulation of Fruit Growth and Abscission. *Acta Horticulturae, 636*, 235-248.

BARDEN, J. A. (1978). Apple leaves, their morphology and photosynthetic potential. . *HortScience, 13*, 644–646.

BASAK, A. (2011). Efficiency of fruitlet thinning in apple 'Gala Must' by use of metamitron and artificial shading. *Journal of Fruit and Ornamental Plant Research, 19*(1), 51-62.

BASSETT, C. L., GLENN, D. M., FORSLINE, P. L., WISNIEWSKI, M. E., & FARRELL, R. E. (2011). Characterizing Water Use Efficiency and Water Deficit Responses in Apple (Malus Xdomestica Borkh. and Malus sieversii Ledeb.) M. Roem. *HortScience, 46*(8), 1079-1084.

BEGG, J. E., & TURNER, N. C. (1970). Water Potential Gradients in Field Tobacco. *Plant Physiology, 46*, 343-346.

BEHBOUDIAN, M. H., DIXON, J., & POTHAMSHETTY, K. (1998). Plant and fruit responses of lysimeter-grown 'Braeburn' apple to deficit irrigation. *Journal of Horticultural Science and Biotechnology, 73*(6), 781-785.

BEHBOUDIAN, M. H., GRAVES, W. R., WALSH, C. S., & KORCAK, R. F. (1994). Water relations, mineral nutrition, growth, and ^{13}C discrimination in two apple cultivars under daily episodes of high root-medium temperature. *Plant and Soil, 162*, 125-133.

BEHBOUDIAN, M. H., MARSAL, J., GIRONA, J., & LOPEZ, G. (2011). Quality and Yield Responses of Deciduous Fruits to Reduced Irrigation. *Horticultural Reviews, 38*, 149-189.

BEIKIRCHER, B., DE CESARE, C., & MAYR, S. (2013). Hydraulics of high-yield orchard trees: a case study of three Malus domestica cultivars. *Tree Physiology, 33*(12), 1296–1307.

BEPETE, M., & LAKSO, A. N. (1997). Apple Fruit Respiration in the Field: Relationship to Fruit Growth Rate, Temperature, and Light Exposure. *Acta Horticulturae, 451*, 319-326.

BEPETE, M., & LAKSO, A. N. (1998). Differential Effects of Shade on Early-season Fruit and Shoot Growth Rates in 'Empire' Apple. *HortScience, 33*(5), 823-825.

BERMAN, M. E., & DEJONG, T. (1997). Diurnal patterns of stem extension growth in peach (Prunus persica): Temperature and fluctuations in water status determine growth rate. *Physiologia Plantarum, 100*, 361-370.

BERÜTER, J., & DROZ, P. (1991). Studies on locating the signal for fruit abscission in the apple tree. *Scientia Horticulturae, 46*(3-4), 201-214.

BÖHNING, R. H. (1948). Time course of photosynthesis in apple leaves exposed to continuous illumination. *Plant Physiology*, 222-240.

BOOTE, K. J., JONES, J. W., & PICKERING, N. B. (1996). Potential Uses and Limitations of Crop Models. *Agronomy Journal, 88*(5), 704-716.

BRADFORD, K. J., & HSIAO, T. C. (1982). Physiological Responses to Moderate Water Stress. *Encyclopedia of Plant Physiology*, 263-324.

BRAUN, P. (2008). Bewässerung beim Kernobst: "Es kommt darauf an!". *Obstbau*(7), 391-394.

BRAUN, P. (2012). Personal Communication.

BRAUN, P., MAURER, B., & HEINEMANN, G. (2000). Scaling Transpiration in apple orchards - Meteorological versus plant based physiological measurements. *Acta Horticulturae, 537*, 45-51.

BRAVIN, E., MONNEY, P., & MENCARELLI HOFMANN, D. (2008). Klimaveränderung: Welche Zunahme der Bewässerungskosten in der Apfelproduktion ist tragbar? *Yearbook of Socioeconomics in Agriculture*, 133-160.

BUBÁN, T., & FAUST, M. (1982). Flower bud induction in apple trees: internal control and differentiation. *Horticultural Reviews, 4*, 174-203.

BUTLER, D. R., & LANDSBERG, J. J. (1981). Respiration rates of apple trees, estimated by CO_2-efflux measurements. *Plant, Cell and Environment, 4*, 153-159.

BUWALDA, J. G. (1991). A mathematical model of carbon acquisition and utilisation by kiwifruit vines. *Ecological Modelling, 57*(1-2), 43-64.

BUWALDA, J. G., & LENZ, F. (1992). Effects of cropping, nutrition and water supply on accumulation and distribution of biomass and nutrients for apple trees on 'M9' root systems. *Physiologia Plantarum, 84*, 21-28.

BUWALDA, J. G., & MEEKINGS, J. S. (1992). Parameter estimation and validation of a canopy photosynthesis model for kiwifruit vines. *Acta Horticulturae, 313*, 29-36.

BUWALDA, J. G., WALTON, E. F., & SMITH, G. S. (1990). A carbon balance model for the kiwifruit vine. *Acta Horticulturae, 276*, 87-95.

BYERS, R. E. (2002). Influence of Temperature and Darkness on Apple Fruit Abscission and Chemical Thinning. *Journal of Tree Fruit Production, 3*(1), 41-53.

BYERS, R. E., BARDEN, J. A., & CARBAUGH, D. H. (1990a). Thinning of Spur 'Delicious' Apples by Shade, Terbacil, Carbaryl, and Ethephon. *Journal of the American Society of Horticultural Science, 115*(1), 9-13.

BYERS, R. E., BARDEN, J. A., POLOMSKI, R. F., YOUNG, R. W., & CARBAUGH, D. H. (1990b). Apple Thinning by Photosynthetic Inhibition. *Journal of the American Society of Horticultural Science, 115*(1), 14-19.

BYERS, R. E., & CARBAUGH, D. H. (2002). Effects of Thinning Time on Yield, Fruit Size, and Return Bloom of '˜Yorkâ' and 'Golden Delicious' Apple Trees. *Journal of Tree Fruit Production, 3*(1), 55 - 62.

CALHEIROS DE MIRANDA, R. A., & BUTLER, D. R. (1986). Interception of rainfall in a hedgerow apple orchard. *Journal of Hydrology, 87*, 245-253.

CAMPBELL, R. J., MARINI, R. P., & BIRCH, J. B. (1992). Canopy Position Affects Light Response Curves for Gas Exchange Charateristics of Apple Spur Leaves. *Journal of the American Society for Horticultural Science, 117*(3), 467-472.

CASADESUS, J., MATA, M., MARSAL, J., & GIRONA, J. (2011). Automated irrigation of apple trees based on measurements of light interception by the canopy. *Biosystems Engineering*(108), 220-226.

CHARLES-EDWARDS, D. A. (1982). Light-Utilization Efficiency. In D. A. Charles-Edwards (Ed.), *Physiological Determinants of Crops Growth* (pp. 65-85). Sydney: Academic Press.

CHEN, K., HU, G. Q., & LENZ, F. (2002). Effects of Doubled Atmospheric CO_2 Concentration on Apple Trees IV. Water Consumption. *Gartenbauwissenschaft, 67*(3), 99-106.

CHEN, K., & LENZ, F. (1997). Effects of Training Method, Shading, and Fruiting on Water Consumption of Apple Trees. *Gartenbauwissenschaft, 62*(6), 277-285.

CHENG, L., & LUO, X. (1997). Diurnal and Seasonal Stomatal Regulation of Water Use Efficiency in Leaves of Field-grown Apple Trees. *Acta Horticulturae, 451*, 375-382.

COHEN, S., & NAOR, A. (2002). The effect of three rootstocks on water use, canopy conductance and hydraulic parameters of apple trees and predicting canopy from hydraulic conductance. *Plant, Cell and Environment, 25*, 17-28.

CORELLI-GRAPPADELLI, L. (2003). Light Relations. In D. C. Ferree & I. J. Warrington (Eds.), *Apples: Botany, Production and Uses* (pp. 195-216). Cambridge: CABI International.

CORELLI-GRAPPADELLI, L., & LAKSO, A. N. (2004). Fruit Development in Deciduous Tree Crops as Affected by Physiological Factors and Environmental Conditions. *Acta Horticulturae, 636*, 425-441.

CORELLI-GRAPPADELLI, L., LAKSO, A. N., & FLORE, J. (1994). Early Season Patterns of Carbohydrate Partitioning in Exposed and Shaded Apple Branches. *Journal of the American Society of Horticultural Sciences, 119*(3), 596-603.

COSTES, E. (2004). Integrating Knowledge of Tree Biology and Physiology into Models of Fruit Tree Development: A Review. *Acta Horticulturae, 636*, 575-589.

COSTES, E., DE REFFYE, P., LICHOU, J., GUÉDON, Y., AUDUBERT, A., & JAY, M. (1992). Stochastic modelling of apricot growth units and branching. *Acta Horticulturae, 313*, 89-98.

COSTES, E., & GUÉDON, Y. (2002). Modelling Branching Patterns on 1-year-old Trunks of Six Apple Cultivars. *Annals of Botany, 89*, 513-524.

COSTES, E., LAURI, P.-E., & REGNARD, J. L. (2006). Analyzing Fruit Tree Architecture: Implications for Tree Management and Fruit Production. *Horticultural Reviews, 32*, 1-61.

COSTES, E., SMITH, C., RENTON, M., GUÉDON, Y., PRUSINKIEWICZ, P., & GODIN, C. (2008). MAppleT: Simulation of Apple Tree Development Using Mixed Stochastic and Biomechanical Models. *Functional Plant Biology, 35*(10), 936-950.

DA SILVA, D., FAVREAU, R., AUZMENDI, I., & DEJONG, T. (2011). Linking water stress effects on carbon partitioning by introducing a xylem circuit into L-PEACH. *Annals of Botany, 108*(6), 1135-1145.

DA SILVA, D., HAN, L., & COSTES, E. (2014). Light interception efficiency of apple trees: A multiscale computational study based on MAppleT. *Ecological Modelling, 290*, 45-53.

DAVIES, F. S., & LAKSO, A. N. (1979). Diurnal and Seasonal Changes in Leaf Water Potential Components and Elastic Properties in Response to Water Stress in Apple Trees. *Physiologia Plantarum, 46*, 109-114.

DAVIES, W. J., & ZHANG, J. (1991). Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology, 42*, 55-76.

DE PURY, D. G. G., & FARQUHAR, G. D. (1997). Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell and Environment, 20*, 537-557.

DE REFFYE, P., HEUVELINK, E., BARTHÉLÉMY, D., COURNÈDE, P. H., SVEN ERIK, J., & BRIAN, F. (2008). Plant Growth Models *Encyclopedia of Ecology* (pp. 2824-2837). Oxford: Academic Press.

DE SWAEF, T., STEPPE, K., & LEMEUR, R. (2009). Determining reference values for stem water potential and maximum daily trunk shrinkage in young apple trees based on plant responses to water deficit. *Agricultural Water Management, 96*(4), 541-550.

DEJONG, T. M., DA SILVA, D., VOS, J., & ESCOBAR-GUTIÉRREZ, A. J. (2011). Using functional–structural plant models to study, understand and integrate plant development and ecophysiology. *Annals of Botany, 108*(6), 987-989.

DEJONG, T. M., & GROSSMAN, Y. L. (1992). Modelling the seasonal carbon economy of deciduous tree crops. *Acta Horticulturae, 313*, 21-28.

DENNIS, F. G. J. (2000). The history of fruit thinning. *Plant Growth Regulation, 31*, 1-16.

DENNIS, F. G. J. (2003). Flowering, Pollination and Fruit Set and Development. In D. C. Ferree & I. J. Warrington (Eds.), *Apples: Botany, Production and Uses* (pp. 153-166). Cambridge: CABI publishing.

DOLTRA, J., ONCINS, J. A., BONANY, J., & COHEN, M. (2007). Evaluation of plant-based water status indicators in mature apple trees under field conditions. *Irrigation Science, 25*, 351-359.

DÖRFLINGER, F. (2010). *Malus domestica 'Gala': An apple with difficulties.* Hochschule Rhein Main.

DRAGONI, D., LAKSO, A. N., & PICCIONI, R. M. (2004). Transpiration of an Apple Orchard in a Cool Humid Climate: Measurement and Modeling. *Acta Horticulturae, 664*, 175-180.

DWD. (2011). Vieljährige Mittelwerte - Geisenheim. Geisenheim: DWD Deutscher Wetterdienst - Abteilung Agrarmeteorologie - Außenstelle Geisenheim - Ehlig, Andreas - 08.02.2011.

EBEL, R. C., PROEBSTING, E. L., & EVANS, R. G. (1995). Deficit Irrigation to Control Vegetative Growth in Apple and Monitoring Fruit Growth to Schedule Irrigation. *HortScience, 30*(6), 1229-1232.

EBEL, R. C., PROEBSTING, E. L., & EVANS, R. G. (2001). Apple Tree and Fruit Responses to Early Termination of Irrigation in a Semi-arid Environment. *HortScience, 36*(7), 1197-1201.

EBEL, R. C., PROEBSTING, E. L., & PATTERSON, M. E. (1993). Regulated Deficit Irrigation May Alter Apple Maturity, Quality, and Storage Life. *HortScience, 28*(2), 141-143.

EBERT, A., & BANGERTH, F. (1982). Possible hormonal modes of action of three apple thinning agents. *Scientia Horticulturae, 16*(4), 343-356.

EVETT, S. R., SCHWARTZ, R. C., CASANOVA, J. J., & HENG, L. K. (2012). Soil water sensing for water balance, ET and WUE. *Agricultural Water Management, 104*(0), 1-9.

EVETT, S. R., TOLK, J. A., & HOWELL, T. A. (2006). Soil Profile Water Content Determination: Sensor Accuracy, Axial Response, Calibration, Temperature Dependence, and Precision. *Vadose Zone Journal, 5*, 894-907.

FALLAHI, E., FALLAHI, B., & SHAFII, B. (2013). Irrigation and Rootstock Influence on Water Use, Tree Growth, Yield, and Fruit Quality at Harvest at Different Ages of Trees in ‘Pacific Gala’ Apple. *HortScience, 48*(5), 588-593.

FALLAHI, E., FALLAHI, B., SHAFII, B., & MORALES, B. (2006). Water Use, Tree Growth and Leaf Mineral Nutrients of Young 'Fuji' Apples as Influenced by Different Irrigation Systems. *Acta Horticulturae, 721*, 63-70.

FALLAHI, E., NEILSEN, D., NEILSEN, G. H., FALLAHI, B., & SHAFII, B. (2010). Efficient Irrigation for Optimum Fruit Quality and Yield in Apples. *HortScience, 45*(11), 1616-1625.

FAN, P. G., LI, L. S., DUAN, W., LI, W. D., & LI, S. H. (2010). Photosynthesis of young apple trees in response to low sink demand under different air temperatures. *Tree Physiology, 30*, 313-325.

FANJUL, L., & ROSHER, P. H. (1984). Effects of water stress on internal water relations of apple leaves. *Physiologia Plantarum, 62*(3), 321-328.

FAOSTAT. (2015). Retrieved 01.03.2015, from http://faostat3.fao.org/search/apple/E

FARQUHAR, G. D., VON CAEMMERER, S., & BERRY, J. A. (1980). A Biochemical Model of Photosynthetic CO_2 Assimilation in Leaves of C_3 Species. *Planta, 149*, 78-90.

FERNANDEZ, R. T., PERRY, R. L., & FLORE, J. A. (1997a). Drought Response of Young Apple Trees on Three Rootstocks. II. Gas Exchange, Chlorophyll Fluorescence, Water Relations, and Leaf Abscisic Acid. *Journal of the American Society for Horticultural Science, 122*(6), 841-848.

FERNANDEZ, R. T., PERRY, R. L., & FLORE, J. A. (1997b). Drought Response of Young Apple Trees on Three Rootstocks: Growth and Development. *Journal of the American Society for Horticultural Science, 122*(1), 14-19.

FLEXAS, J., BARBOUR, M. M., BRENDEL, O., CABRERA, H. M., CARRIQUÍ, M., DÍAZ-ESPEJO, A., et al. (2012). Mesophyll diffusion conductance to CO2: An unappreciated central player in photosynthesis. *Plant Science, 193–194*, 70-84.

FLEXAS, J., BOTA, J., CIFRE, J., MARIANO ESCALONA, J., GALMÉS, J., GULÍAS, J., et al. (2004). Understanding down-regulation of photosynthesis under water stress: future prospects and searching for physiological tools for irrigation management. *Annals of Applied Biology, 144*(3), 273-283.

FLORE, J., & LAKSO, A. N. (1990). Environmental and Physiological Regulation of Photosynthesis in Fruit Crops. *Horticultural Reviews, 11*, 111-157.

FLORE, J., LAKSO, A. N., & MOON, J. W. (1985). The effect of water stress and vapor pressure gradient on stomatal conductance, water use efficiency, and photosynthesis of fruit crops. *Acta Horticulturae, 171*, 207-218.

FORSHEY, C. G., & ELFVING, D. C. (1989). The Relationship Between Vegetative Growth and Fruiting in Apple Trees. *Horticultural Reviews, 11*, 229-287.

FOSTER, T., JOHNSTON, R., & SELEZNYOVA, A. (2003). A Morphological and Quantitative Characterization of Early Floral Development in Apple (*Malus X domestica* Borkh.). *Annals of Botany, 92*, 199-206.

FRIEND, A. D. (2001). Modelling canopy CO_2 fluxes: are 'big-leaf' simplifications justified? *Global Ecology and Biogeography, 10*, 603-619.

FUJII, J. A., & KENNEDY, R. A. (1985). Seasonal Changes in the Photosynthetic Rate in Apple Trees. *Plant Physiology, 78*, 519-524.

GARCÍA PETILLO, M., PUPPO, L., MORALES, P., & HAYASHI, R. (2011). Young Apple Trees Responses to Water Stress - Early Results. *Acta Horticulturae, 889*, 273-280.

GINDABA, J., & WAND, S. J. E. (2007). Climate-ameliorating measures influence photosynthetic gas exchange of apple leaves. *Annals of Applied Biology, 150*(1), 75-80.

GIRONA, J., BEHBOUDIAN, M. H., MATA, M., DEL CAMPO, J., & MARSAL, J. (2010). Exploring six reduced irrigation options under water shortage for [`]Golden Smoothee' apple: Responses of yield components over three years. *Agricultural Water Management, 98*(2), 370-375.

GIRONA, J., DEL CAMPO, J., MATA, M., LOPEZ, G., & MARSAL, J. (2011). A comparative study of apple and pear tree water consumption measured with two weighing lysimeters. *Irrigation Science, 29*, 55-63.

GOFFINET, M. C., ROBINSON, T. L., & LAKSO, A. N. (1995). A comparison of 'Empire' apple fruit size and anatomy in unthinned and hand-thinned trees. *Journal of Horticultural Science, 70*(3), 375-387.

GOLDSCHMIDT, E. E., & LAKSO, A. N. (2005). Fruit Tree Models: Scope and Limitations. In E. Gelb & A. Offer (Eds.), *Information and Communication Technology (ICT) Development and Adoption: Perspectives of Technological Innovation* (pp. 1-19).

GÖLLES, M., & WIDMER, A. (2012). Modell "Greene" zur Prognose des Fruchtansatzes bei Äpfeln. *Schweizer Zeitschrift für Obst- und Weinbau, 18*, 11-14.

GONG, D., KANG, S., ZHANG, L., DU, T., & YAOM, L. (2006). A two-dimensional model of root water uptake for single apple trees and its verification with sap flow and soil water content measurements. *Agricultural Water Management, 83*, 119-129.

GONZÁLEZ-TALICE, J., YURI, J. A., LEPE, V., HIRZEL, J., & DEL POZO, A. (2012). Water use in three apple cultivars from the second season to sixth season in a drainage lysimeter. *Scientia Horticulturae, 146*, 131-136.

GOODE, J. E., & HIGGS, K. H. (1973). Water, osmotic and pressure potential relationships in apple leaves. *Journal of Horticultural Science, 48*, 203-215.

GOWING, D. J. G., DAVIES, W. J., & JONES, H. G. (1990). A Positive Root-sourced Signal as an Indicator of Soil Drying in Apple, *Malus x domestica* Borkh. *Journal of Experimental Botany, 41*(233), 1535-1540.

GREEN, S., & CLOTHIER, B. (1999). The root zone dynamics of water uptake by a mature apple tree. *Plant and Soil, 206*, 61-77.

GREEN, S., MCNAUGTON, K., WÜNSCHE, J. N., & CLOTHIER, B. (2003). Modeling Light Interception and Transpiration of Apple Tree Canopies. *Agronomy Journal, 95*, 1380-1387.

GREEN, S. R., KIRKHAM, M. B., & CLOTHIER, B. E. (2006). Root uptake and transpiration: From measurements and models to sustainable irrigation. *Agricultural Water Management, 86*, 165-176.

GREEN, S. R., & MCNAUGTON, K. (1997). Modelling effective stomatal resistance for calculating transpiration from an apple tree. *Agricultural and Forest Meteorology, 83*, 1-26.

GREENE, D. W. (2002). Chemicals, Timing, and Environmental Factors Involved in Thinner Efficacy on Apple. *HortScience, 37*(3), 477-481.

GREENE, D. W. (2006). Effect of Auxin Inhibitors on Fruit Growth and Fruit Set of 'McIntosh', 'Delicious' and 'Golden Delicious' Apples. *Acta Horticulturae, 727*, 255-262.

GREENE, D. W. (2008). A Growers Guide to Predicting the Response to a Chemical Thinner Application. Retrieved 17.03.2015, from http://fruitadvisor.info/tfruit/2008/predictthinprocedure.pdf

GREENE, D. W., KRUPA, J., VEZINA, M., LAKSO, A. N., & ROBINSON, T. L. (2005). A Method to Predict Chemical Thinner Response on Apples. *FruitNotes, 70*, 12-17.

GREENE, D. W., LAKSO, A. N., ROBINSON, T. L., & SCHWALLIER, P. (2013). Development of a Fruitlet Growth Model to Predict Thinner Response on Apples. *HortScience, 48*(5), 584-587.

GUAK, S., BEULAH, M., & LOONEY, N. E. (2004). Thinning of 'Fuji' and 'Gala' Apples with Lime Sulphor and other Chemicals *Acta Horticulturae 636*, 339-346.

HAMACHER, M., BLANKE, M. M., & LENZ, F. (1994). Diurnal CO_2 fluctuations in an apple orchards. *Environmental and Experimental Botany, 34*(4), 385-391.

HANDSCHACK, M. (1997). Fruchtfall beim Apfel. *Obstbau, 6*, 286-290.

HÄTTASCH, C., FLACHOWSKY, H., KAPTURSKA, D., & HANKE, M.-V. (2008). Isolation of flowering genes and seasonal changes in their transcript levels related to flower induction and initiation in apple (Malus domestica). *Tree Physiology, 28*(10), 1459-1466.

HSIAO, T. C. (1973). Plant Responses to Water Stress. *Annual Review of Plant Physiology, 24*, 519-570.

HUGHES, K. A., & GANDAR, P. W. (1993). Length densities, occupancies and weights of apple root systems. *Plant and Soil, 148*, 211-221.

IANCU, M. (1985). Growth rate of apple trunk and fruit - additional indicators for water needs of fruit trees. *Acta Horticulturae, 171*, 417-425.

IANCU, M., STANICA, F., DUMITRASCU, M., & ISAC, I. (2011). Influence of the Groundcover Management System and Drip Irrigation on Behavior of the 'Golder Spur' apple Cultivar Grafted on MM106. *Acta Horticulturae, 889*, 265-272.

IMMIK, E. (2008). Bewässerungssteuerung - so viel wie nötig, so wenig wie möglich. *Obstbau*(7), 388-390.

INTRIGLIOLO, D. S., & CASTEL, J. R. (2004). Continuous measurement of plant and soil water status for irrigation scheduling in plum. *Irrigation Science, 23*, 93-102.

IWANAMI, H., MORIYA-TANAKA, Y., HONDA, C., WADA, M., MORIYA, S., OKADA, K., et al. (2012). Relationships among apple fruit abscission, source strength, and cultivar. *Scientia Horticulturae, 146*, 39-44.

JACKSON, J. E. (1980). Light Interception and Utilization by Orchard Systems. *Horticultural Reviews, 2*, 208-267.

JACKSON, J. E. (2003). *Biology of Apples and Pears*. Cambridge, UK: Cambridge University Press.

JACKSON, J. E., & PALMER, J. (1980). A computer model study of light interception by orchards in relation to mechanised harvesting and management. *Scientia Horticulturae, 13*, 1-7.

JACKSON, J. E., & PALMER, J. W. (1977). Effects of shade on the growth an cropping of apple trees. I. Experimental details and effects on vegetative growth II. Effects on components of yield III.Effects on fruit growth, chemical composition and quality at harvest and after storage. *Journal of Horticultural Science, 52*, 245-282.

JACKSON, J. E., & PALMER, J. W. (1979). A Simple Model of Light Transmission and Interception by Discontinuous Canopies. *Annals of Botany, 44*, 381-383.

JIE, Z., YUNCONG, Y., STREETER, J. G., & FERREE, D. C. (2010). Influence of soil drought stress on photosynthesis, carbohydrates and the nitrogen and phosphorus absorb in different section of leaves and stem of Fugi/M.9EML, a young apple seedling. *African Journal of Biotechnology, 9*(33), 5320-5325.

JOHNSON, R. S., & LAKSO, A. N. (1985). Relationships between Stem Length, Leaf Area, Stem Weight, and Accumulated Growing Degree-days in Apple Shoots. *Journal of the American Society of Horticultural Sciences, 110*(4), 586-590.

JONES, H. G. (1985). Partitioning stomatal and non-stomatal limitations to photosynthesis. *Plant, cell & environment, 8*(2), 95-104.

JONES, H. G. (2004). Irrigation scheduling: advantages and pitfalls of plant-based methods. *Journal of Experimental Botany, 55*(407).

JONES, H. G. (2014a). *Plants and microclimate* (3 ed.): Cambridge University Press.

JONES, H. G. (2014b). *Plants and Microclimate - A Quantitative Approach to Environmental Plant Physiology* (3 ed.). Cambridge: Cambridge University Press, UK.

JONES, H. G., & FANJUL, L. (1983). Effects of Water Stress on CO2 Exchange in Apple. In R. Marcelle, H. Clijsters & M. van Poucke (Eds.), *Effects of Stress on Photosynthesis* (Vol. 3, pp. 75-84): Springer Netherlands.

JONES, H. G., LAKSO, A. N., & SYVERTSEN, J. P. (1985). Physiological Control of Water Status in Temperate and Subtropical Fruit Trees. *Horticultural Reviews, 7*, 301-344.

JONES, H. G., MASSACCI, A., CORLETT, J., MASOJIDEK, J., & HALL, D. (1990). Use of combined fluorescence and gas-exchange measurements to assess processes limiting photosynthesis under stress. *Bulletin de la Société botanique de France, 137*(1), 67-72.

JONES, H. G., & TARDIEU, F. (1998). Modelling water relations of horticultural crops: a review. *Scientia Horticulturae, 74*, 21-46.

KENNEDY, R., & JOHNSON, D. (1981). Changes in photosynthetic characteristics during leaf development in apple. *Photosynthesis Research, 2*(3), 213-223.

KILILI, A. W., BEHBOUDIAN, M. H., & MILLS, T. M. (1996a). Composition and quality of [`]Braeburn' apples under reduced irrigation. *Scientia Horticulturae, 67*(1-2), 1-11.

KILILI, A. W., BEHBOUDIAN, M. H., & MILLS, T. M. (1996b). Water Relations, Photosynthesis, Growth, and Yield of 'Braeburn' Apples under Reduced Irrigatin Applied at Different Stages of the Growing Season. *Gartenbauwissenschaft, 61*(6), 267-273.

KLAGES, K., DONNISON, H., WÜNSCHE, J., & BOLDINGH, H. (2001). Diurnal changes in non-structural carbohydrates in leaves, phloem exudate and fruit in 'Braeburn' apple. *Australian Journal of Plant Physiology, 28*, 131-139.

KULL, O., & KRUIJT, B. (1999). Acclimation of photosynthesis to light: a mechanistic approach. *Functional Ecology, 13*, 24-36.

LAKSO, A. N. (1979). Seasonal changes in stomatal response to leaf water potential in apple. *Journal of the American Society for Horticultural Science, 104*, 58-60.

LAKSO, A. N. (1985). The effects of water stress on physiological processes in fruit crops. *Acta Horticulturae, 171*, 275-290.

LAKSO, A. N. (1986). Photosynthesis in fruit trees in relation to environmental factors. In A. N. Lakso & F. Lenz (Eds.), *The Regulation of Photosynthesis in Fruit Trees*. Symp Proc Publ, NY State Agric Exp Sta, Geneva, NY, USA: 6-13: Found in: Tromp, J. (2005). Metabolic processes. In: J. Tromp, A. Webster & S. J. Wertheim (Eds.), Fundamentals of Temperate Zone Tree Fruit Production (pp. 39-54). Leiden, The Netherlands: Backhuys Publishers.

LAKSO, A. N. (1992). The simplified dry matter production model for apple: estimation of canopy photosynthesis in discontinuous canopies. *Acta Horticulturae, 313*, 45-51.

LAKSO, A. N. (1994). Apple. In B. Schaffer & P. C. Andersen (Eds.), *Environmental physiology of fruit crops. Vol 1: Temperate crops*. Boca Raton, FL: CRC Press.

LAKSO, A. N. (2003). Water Relations of Apples. In D. C. Ferree & I. J. Warrington (Eds.), *Apples: Botany, Production and Uses* (pp. 167-194). Cambridge: CABI Publishing.

LAKSO, A. N. (2011). Early Fruit Growth and Drop - the Role of Carbon Balance in the Apple Tree. *Acta Horticulturae, 903*, 733-742.

LAKSO, A. N. (2012). Personal Communication.

LAKSO, A. N. (2014). Comparing water use efficiency of apples and grapes – physiological and morphological aspects. *Acta Horticulturae, 1038*, 67-72.

LAKSO, A. N. (2019). Personal Communication.

LAKSO, A. N., CORELLI-GRAPPADELLI, L., BARNARD, J., & GOFFINET, M. C. (1995). An expolinear model of the growth pattern of the apple fruit. *Journal of Horticultural Science, 70*(4), 389-394.

LAKSO, A. N., CORELLI-GRAPPADELLI, L., WÜNSCHE, J., & ROBINSON, T. (1997). Understanding apple tree productivity - balancing carbohydrate supply and demand. *Compact Fruit Tree, 30*, 11-17.

LAKSO, A. N., & DENNING, S. S. (1996). Seasonal bioenergetic construction costs of apple fruits, leaves and shoots. *Acta Horticulturae, 416*, 163-168.

LAKSO, A. N., GEYER, A. S., & CARPENTER, S. G. (1984). Seasonal Osmotic Relations in Apple Leaves of Different Ages. *Journal of the American Society for Horticultural Science, 109*(4), 544-547.

LAKSO, A. N., GREENE, D. W., & PALMER, J. W. (2006a). Improvements on an Apple Carbon Balance Model. *Acta Horticulturae, 707*, 57-61.

LAKSO, A. N., & JOHNSON, R. S. (1990). A simplified dry matter production model for apple using automatic programming simulation software. *Acta Horticulturae, 276*, 141-148.

LAKSO, A. N., & MUSSELMAN, R. C. (1976). Effects of Cloudiness on Interior Diffuse Light in Apple Trees. *Journal of the American Society of Horticultural Sciences, 101*(6), 642-644.

LAKSO, A. N., & NYROP, J. P. (2002). Carbon Balance Modeling Approaches to Integrating the Effects of Foliar Pests, Environment, and Cultural Practices in Apples. *Acta Horticulturae, 584*, 221-228.

LAKSO, A. N., & ROBINSON, T. (2015). Decision Support for Apple Thinning Based on Carbon Balance Modeling. *Acta Horticulturae, 1068*.

LAKSO, A. N., ROBINSON, T., & GREENE, D. W. (2007). Using an Apple Tree Carbohydrate Model to Understand Thinning Responses to Weather and Chemical Thinners. *New York Fruit Quarterly, 15*(3), 16-19.

LAKSO, A. N., & ROBINSON, T. L. (2014). Personal communication.

LAKSO, A. N., ROBINSON, T. L., GOFFINET, M. C., & WHITE, M. D. (2001a). Apple Fruit Growth Responses to varying Thinning Methods and Timing. *Acta Horticulturae, 557*, 407-412.

LAKSO, A. N., ROBINSON, T. L., & GREENE, D. W. (2006b). Integration of Environment, Physiology and Fruit Abscission via Carbon Balance Modeling - Implications for Understanding Growth Regulator Responses. *Acta Horticulturae, 727*, 321-326.

LAKSO, A. N., WHITE, M. D., & TUSTIN, D. S. (2001b). Simulation modelling of the effects of short and long-term climatic variations on carbon balance of apple trees. *Acta Horticulturae, 557*, 473-480.

LAKSO, A. N., WÜNSCHE, J. N., PALMER, J. W., & CORELLI-GRAPPADELLI, L. (1999). Measurement and Modeling of Carbon Balance of the Apple Tree. *HortScience, 34*(6), 1040-1047.

LANDSBERG, J. J., BEADLE, C. L., BISCOE, P. V., BUTLER, D. R., DAVIDSON, B., INCOLL, L. D., et al. (1975). Diurnal Energy, Water and CO2 Exchanges in an Apple (Malus pumila) Orchard. *Journal of Applied Ecology, 12*(2), 659-684.

LANDSBERG, J. J., & JONES, H. G. (1981). Apple Orchards. In T. T. Kozlowski (Ed.), *Water Deficits and Plant Growth* (Vol. VI, pp. 419-469): Academic Press, New York, USA.

LAURI, P.-E., BARIGAH, T. S., LOPEZ, G., MARTINEZ, S., LOSCIALE, P., ZIBORDI, M., et al. (2016). Genetic variability and phenotypic plasticity of apple morphological responses to soil water restriction in relation with leaf functions and stem xylem conductivity. *Trees, 30*(5), 1893-1908.

LAURI, P.-E., BOURDEL, G., TROTTIER, C., & COCHARD, H. (2008). Apple shoot architecture: evidence for strong variablity of bud size and composition and hydraulics within a branching zone. *New Phytologist, 178*, 798-807.

LAURI, P.-E., & KELNER, J. J. (2001). Shoot type demography and dry matter partitioning: a morphometric approach in apple (*Malus xDomestica*). *Canadian Journal of Botany, 79*, 1270-1273.

LAWLOR, D. W. (2002). Limitation to Photosynthesis in Water-stressed Leaves: Stomata vs. Metabolism and the Role of ATP. *Annals of Botany, 89*(7), 871-885.

LE ROUX, X., LACOINTE, A., ESCOBAR-GUTIÉRREZ, A., & LE DIZÈS, S. (2001). Carbon-based models of individual tree growth: A critical appraisal. *Annals of Forest Science, 58*, 469-506.

LEBESE, T. C., WAND, S. J. E., & STASSEN, P. J. C. (2008). Apple Leaf Gas Exchange Measurements in 'Brookfield Gala' in Trees Under Three Water and Nutrient Management Strategies. *Acta Horticulturae, 772*, 41-50.

LEIB, B. G., CASPARI, H. W., REDULLA, C. A., ANDREWS, P. K., & JABRO, J. J. (2006). Partial rootzone drying and deficit irrigation of 'Fuji' apples in a semi-arid climate. *Irrigation Science, 24*, 85-99.

LENTZ, W. (1998). Model applications in horticulture: a review. *Scientia Horticulturae, 74*, 151-174.

LESPINASSE, Y. (1992). Le pommier. In A. Gallais & H. Bannerot (Eds.), *Amélioration des espèces végétales cultivées.* (pp. 579–594). Paris: INRA.

LEVIN, I., ASSAF, R., & BRAVDO, B. (1979). Soil moisture and root distribution in an apple orchard irrigated by tricklers. *Plant and Soil, 52*, 31-40.

LINDENMAYER, A. (1968). Mathematical Models for Cellular Interactions in Development I. Filaments with One-sided Inputs. *Journal of Theoretical Biology, 18*, 280-299.

LINK, H. (1978). Results of Thinning Apples with some Chemical Compounds. *Acta Horticulturae, 80*, 283-286.

LINK, H. (2000). Significance of flower and fruit thinning on fruit quality. *Plant Growth Regulation, 31*(1), 17-26.

LLOYD, J., GRACE, J., MIRANDA, A. C., MEIR, P., WONG, S. C., MIRANDA, H. S., et al. (1995). A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. *Plant, Cell and Environment, 18*, 1129-1145.

LO BIANCO, R., TALLUTO, G., & FARINA, V. (2012). Effects of partial rootzone drying and rootstock vigour on dry matter partitioning of apple trees (*Malus domestica* cvar Pink Lady). *Journal of Agricultural Science, 150*, 75-86.

LOBO, F. D. A., DE BARROS, M. P., DALMAGRO, H. J., DALMOLIN, Â. C., PEREIRA, W. E., DE SOUZA, É. C., et al. (2013). Fitting net photosynthetic light-response curves with Microsoft Excel — a critical look at the models. *Photosynthetica, 51*(3), 445-456.

LOESCHER, W. H., MARLOW, G. C., & KENNEDY, R. A. (1982). Sorbitol Metabolism and Sink-Source Interconversions in Developing Apple Leaves. *Plant Physiology, 70*, 335-339.

LOMBARDINI, L., CASPARI, H. W., ELFVING, D. C., AUVIL, T., & MCFERSON, J. R. (2004). Gas Exchange and Water Relations in 'Fuji' Apple Trees Grown under Deficit Irrigation. *Acta Horticulturae, 636*, 43-50.

LOMBARDINI, L., TOSELLI, M., & FLORE, J. A. (2001). Carbon Translocation and Root Respiration in Potted Apple Trees During Conditions of Moderate Drought. *Acta Horticulturae, 557*, 413-419.

LOPEZ, G., FAVREAU, R. R., SMITH, C., COSTES, E., PRUSINKIEWICZ, P., & DEJONG, T. (2008a). Integrating simulation of architectural development and source-sink behaviour of peach trees by incorporating Markov chains and physiological organ function sub-models into L-PEACH. *Functional Plant Biology, 35*, 761-771.

LOPEZ, G., SMITH, C., FAVREAU, R., & DEJONG, T. (2008b). Using L-PEACH for Dynamic Simulation of Source-Sink Behavior of Peach Trees: Effects of Date of Thinning on Fruit Growth. *Acta Horticulturae, 803*, 209-216.

MAGGS, D. H. (1961). Changes in the Amount and Distribution of Increment Induced by Contrasting Watering, Nitrogen, and Environmental Régimes. *Annals of Botany, 25*(3), 353-361.

MARCELIS, L. F. M., HEUVELINK, E., & GOUDRIAAN, J. (1998). Modelling biomass production and yield of horticultural crops: a review. *Scientia Horticulturae, 74*, 83-111.

MARINI, R. P., & BARDEN, J. A. (1981). Seasonal correlations of specific leaf weight to net photosynthesis and dark respiration of apple leaves. *Photosynthesis Research, 2*, 251-258.

MARSAL, J., JOHNSON, S., CASADESUS, J., LOPEZ, G., GIRONA, J., & STÖCKLE, C. (2014). Fraction of canopy intercepted radiation relates differently with crop coefficient depending on the season and the fruit tree species. *Agricultural and Forest Meteorology, 184*(0), 1-11.

MARSAL, J., LOPEZ, G., MATA, M., ARBONES, A., & GIRONA, J. (2004). Recommendations for Water Conservation in Peach Orchards in Mediterranean Climate Zones using Combined Regulated Deficit Irrigation. *Acta Horticulturae, 664*, 391-397.

MARSAL, J., & STÖCKLE, C. O. (2012). Use of CropSyst as a decision support system for scheduling regulated deficit irrigation in a pear orchard. *Irrigation Science, 30*(2), 139-147.

MASSONNET, C., COSTES, E., RAMBAL, S., DREYER, E., & REGNARD, J.-L. (2007). Stomatal Regulation of Photosynthesis in Apple Leaves: Evidence for Different Water-use Strategies between Two Cultivars. *Annals of Botany, 100*, 1347-1356.

MASSONNET, C., REGNARD, J.-L., COSTES, E., SINOQUET, H., & AMÉGLIO, T. (2006). Parameterization of the Functional-Structural RATP Model for Apple Trees: Application to Simulate Photosynthesis and Transpiration of Fruiting Branches. *Acta Horticulturae, 707*, 77-84.

MASSONNET, C., REGNARD, J.-L., LAURI, P.-E., COSTES, E., & SINOQUET, H. (2008). Contributions of foliage distribution and leaf functions to light interception, transpiration and photosynthetic capacities in two apple cultivars at branch and tree scales. *Tree Physiology, 28*, 665-678.

MCCUTCHAN, H., & SHACKEL, K. A. (1992). Stem-water Potential as a Sensitive Indicator of Water Stress in Prune Trees (*Prunus domestica* L. cv. French). *Journal of the American Society for Horticultural Science, 117*(4), 607-611.

MEDRANO, H., ESCALONA, J. M., BOTA, J., GULIAS, J., & FLEXAS, J. (2002). Regulation of Photosynthesis of C3 Plants in Response to Progressive Drought: Stomatal Conductance as a Reference Parameter. *Annals of Botany, 89*(7), 895-905.

MEIER, U. (2001). *BBCH: Growth stages of mono- and dicotyledonous plants.* Federal Biological Research Centre for Agriculture and Forestry, Bonn.

MIEROWSKA, A., KEUTGEN, N., HUYSAMER, M., & SMITH, V. (2002). Photosynthetic acclimation of apple spur leaves to summer-pruning. *Scientia Horticulturae, 92*(1), 9-27.

MILLS, T. M., BEHBOUDIAN, M. H., & CLOTHIER, B. E. (1996). Water Relations, Growth, and the Composition of 'Braeburn' Apple Fruit under Deficit Irrigation. *Journal of the American Society for Horticultural Science, 121*(2), 286-291.

MILLS, T. M., HOSSEIN BEHBOUDIAN, M., & CLOTHIER, B. E. (1997). The diurnal and seasonal water relations, and composition, of `Braeburn' apple fruit under reduced plant water status. *Plant Science, 126*(2), 145-154.

MONSELISE, S. P., & LENZ, F. (1980). Effect of Fruit Load on Stomatal Resistance, Specific Leaf Weight, and Water Content of Apple Leaves. *Gartenbauwissenschaft, 45*(4), 188-191.

MPELASOKA, B. S., & BEHBOUDIAN, M. H. (2002). Production of aroma volatiles in response to deficit irrigation and to crop load in relation to fruit maturity for [`]Braeburn' apple. *Postharvest Biology and Technology, 24*(1), 1-11.

MPELASOKA, B. S., BEHBOUDIAN, M. H., DIXON, J., NEAL, S., & CASPARI, H. W. (2000a). Improvement of fruit quality and storage potential of 'Braeburn' apple through deficit irrigation. *Journal of Horticultural Science and Biotechnology, 75*(5), 615-621.

MPELASOKA, B. S., BEHBOUDIAN, M. H., & GREEN, S. R. (2000b). Effects of irrigation regime and crop load on water use and yield of 'braeburn' apple grown in lysimeters. *Acta Horticulturae, 537*, 741-748.

MPELASOKA, B. S., BEHBOUDIAN, M. H., & MILLS, T. M. (2001). Water relations, photosynthesis, growth, yield and fruit size of 'Braeburn' apple: Responses to deficit irrigation and to crop load. *Journal of Horticultural Science and Biotechnology, 76*(2), 150-156.

NAOR, A. (1998). Relations between leaf and stem water potentials and stomatal conductance in three field-grown woody species. *Journal of Horticultural Science & Biotechnology, 73*(4), 431-436.

NAOR, A. (2000). Midday stem water potential as a plant water stress indicator for irrigation scheduling in fruit trees. *Acta Horticulturae, 537*, 447-454.

NAOR, A. (2006). Irrigation Scheduling and Evaluation of Tree Water Status in Deciduous Orchards. *Horticultural Reviews, 32*, 111-165.

NAOR, A. (2008). Water Stress Assessment for Irrigation Scheduling of Deciduous Trees. *Acta Horticulturae, 792*, 467-482.

NAOR, A. (2014). Crop Load and Irrigation Interactions - A New Dimension of RDI. *Acta Horticulturae, 1038*, 113-119.

NAOR, A., & COHEN, S. (2003). Sensitivity and Variability of Maximum Trunk Shrinkage, Midday Stem Water Potential, and Transpiration Rate in Response to Withholding Irrigation from Field-grown Apple Trees. *HortScience, 38*(4), 547-551.

NAOR, A., KLEIN, I., & DORON, I. (1995). Stem Water Potential and Apple Size. *Journal of the American Society for Horticultural Science, 120*(4), 577-582.

NAOR, A., KLEIN, I., DORON, I., GAL, Y., BEN-DAVID, Z., & BRAVDO, B. (1997). The effect of irrigation and crop load on stem water potential and apple fruit size. *Journal of Horticultural Science, 72*(5), 765-771.

NAOR, A., NASCHITZ, S., PERES, M., & GAL, Y. (2008). Responses of apple fruit size to tree water status and crop load. *Tree Physiology, 28*, 1255-1261.

NASCHITZ, S., NAOR, A., GENISH, S., WOLF, S., & GOLDSCHMIDT, E. E. (2010). Internal management of non-structural carbohydrate resources in apple leaves and branch wood under a broad range of sink and source manipulations. *Tree Physiology, 30*(6), 715-727.

NEILSEN, D., & NEILSEN, G. H. (2002). Efficient Use of Nitrogen and Water in High-density Apple Orchards. *HortTechnology, 12*(1), 19-25.

NEMESKÉRI, E. (2007). Water relations of apple and influence on fruit quality (minireview). *International Journal of Horticultural Science, 13*(3), 59-63.

NEWA CORNELL UNIVERSITY. (2015). Apple Carbohydrate Thinning. Retrieved 15.06.2015, 2015, from http://newa.cornell.edu/index.php?page=apple-thin; http://newa.nrcc.cornell.edu/apple_thin_help.html

O'CONNELL, M. G., & GOODWIN, I. (2007). Responses of 'Pink Lady' apple to deficit irrigation and partial rootzone drying: physiology, growth, yield, and fruit quality. *Australian Journal of Agricultural Research, 58*, 1068-1076.

O'CONNELL, M. G., GOODWIN, I., & WHEATON, A. D. (2008). Response of Pink Lady Apple to Irrigation Estimated from Effective Area of Shade. *Acta Horticulturae, 792*, 495-502.

OLIEN, W. C., & LAKSO, A. N. (1986). Effect of rootstock on apple (*Malus domestica*) tree water relations. *Physiologia Plantarum, 67*, 421-430.

OYARZUN, R. A., STÖCKLE, C. O., & WHITING, M. D. (2007). A simple approach to modeling radiation interception by fruit-tree orchards. *Agricultural and Forest Meteorology, 142*(1), 12-24.

PAGAY, V., SANTIAGO, M., SESSOMS, D. A., HUBER, E. J., VINCENT, O., PHARKYA, A., et al. (2014). A microtensiometer capable of measuring water potentials below -10 MPa. [10.1039/C4LC00342J]. *Lab on a Chip, 14*(15), 2806-2817.

PALMER, J. W. (1977). Light transmittance by apple leaves and canopies. *Journal of Applied Ecology, 14*, 505-513.

PALMER, J. W. (1986). Light interception and dry matter production by apple orchards. In A. N. Lakso & F. Lenz (Eds.), *The regulation of photosynthesis in fruit trees* (Vol. Special Publication). Geneva: New York State Agricultural Experiment Station.

PALMER, J. W. (1988). Annual Dry Matter Production and Partitioning over the first 5 years of a bed system of Crispin/M.27 apple trees at four spacings. *Journal of Applied Ecology, 25*, 569-578.

PALMER, J. W. (1989a). Canopy manipulation for optimum utilization of light. *Easter School in Agricultural Science, 47*, 245-262.

PALMER, J. W. (1989b). The effects of row orientation, tree height, time of year and latitude on light interception and distribution in model apple hedgerow canopies. *Journal of Horticultural Science, 64*(2), 137-145.

PALMER, J. W. (1992). Effects of varying crop load on photosynthesis, dry matter production and partitioning of Crispin/M.27 apple trees. *Tree Physiology, 11*, 19-33.

PALMER, J. W., GIULIANI, R., & ADAMS, H. M. (1997). Effect of crop load on fruiting and leaf photosynthesis of 'Braeburn'/M.26 apple trees. *Tree Physiology, 17*, 741-746.

PAN, Q., WANG, Z., & QUEBEDEAUX, B. (1998). Responses of apple plant to CO_2 enrichment: changes in photosynthesis, sorbitol, other soluble sugars, and starch. *Australian Journal of Plant Physiology, 25*, 293-297.

PARRA-QUEZADA, R. A., ROBINSON, T., OSBORNE, J. L., LAKSO, A. N., & PARRA-BUJANDA, L. B. (2006). Temperature and Chemical Thinner Affect Fruit Set, and Growth of 'Empire' Apple. *Acta Horticulturae, 727*, 327-336.

PENN STATE UNIVERSITY. (2015). Cornell MaluSim Model. Retrieved 26.06.2015, 2015, from http://extension.psu.edu/plants/tree-fruit/news/2012/a-new-tool-for-apple-cropload-management-cornell-malusim-model-for-determining-carbon-balance-in-apple-trees; http://extension.psu.edu/plants/tree-fruit/news/2015/precision-crop-load-management-and-the-2015-malusim-carbohydrate-model-operation

PEREIRA, A. R., GREEN, S. R., & NOVA, N. A. V. (2007). Sap flow, leaf area, net radiation and the Priestley-Taylor formula for irrigated orchards and isolated trees. *Agricultural Water Management, 92*(1-2), 48-52.

PFEIFER, T. M. (2012). *Gezielte Ertragsregulierung bei Äpfeln unter Berücksichtigung natürlicher Fruchtfälle.* Master-Thesis, Hochschule Rhein-Main, Geisenheim.

PFEIFFER, B., & RUEß, F. (2002). *Screening of agents for thinning blossoms of apple trees.* Paper presented at the Proc. 10th Int. Conf. Cultivation technique and phytopathological problems in organic fruitgrowing and viticulture.

POWELL, D. B. B. (1974). Some effects of water stress in late spring on apple trees. *Journal of Horticultural Science, 49*, 257-272.

POWELL, D. B. B. (1976). Continuous Measurement of Shoot Extension and Stem Expansion in the Field. *Journal of Experimental Botany, 27*(6), 1361-1369.

PRETORIUS, J. J. B. (2006). *9. Late-season stomatal sensitivity to microclimate is influenced by sink strength and soil moisture stress in 'Braestar' apple trees in South Africa.* Dissertation.

PRETORIUS, J. J. B., & WAND, S. J. E. (2003). Late-season stomatal sensitivity to microclimate is influenced by sink strength and soil moisture stress in 'Braestar' apple trees in South Africa. *Scientia Horticulturae, 98*, 157-171.

PRUSINKIEWICZ, P. (1997). A Look at the Visual Modeling of Plants Using L-Systems. In R. L. Hofestädt, T.; Löffler, M.; Schomburg, D. (Ed.), *Bioinformatics. GCB 1996. Lecture Notes in Computer Science* (Vol. 1278). Berlin, Heidelberg: Springer.

PRUSINKIEWICZ, P. (2004). Modeling plant growth and development. *Current Opinion in Plant Biology, 7*(1), 79-83.

PRUSINKIEWICZ, P., & RUNIONS, A. (2012). Computational models of plant development and form. *New Phytologist, 193*(3), 549-569.

PSARRAS, G., & MERWIN, I. A. (2000). Water Stress Affects Rhizosphere Respiration Rates and Root Morphology of Young `Mutsu' Apple Trees on M.9 and MM.111 Rootstocks. *Journal of the American Society for Horticultural Science, 125*(5), 588-595.

RAMÍREZ, F., & DAVENPORT, T. L. (2013). Apple pollination: A review. *Scientia Horticulturae, 162*, 188-203.

RAUPACH, M. R., & FINNIGAN, J. J. (1988). 'Single-layer Models of Evaporation from Plant Canopies are Incorrect but Useful, Whereas Multilayer Models are Correct but Useless': Dicuss. *Australian Journal of Plant Physiology, 15*, 705-716.

RENTON, M., COSTES, E., GUÉDON, Y., & GODIN, C. (2006). Integrating Makov Chain Models and L-systems to Simulate the Architectural Development of Apple Trees. *Acta Horticulturae, 707*, 63-80.

REYES, V. M., GIRONA, J., & MARSAL, J. (2006). Effect of late Spring defruiting on net CO_2 exchange and leaf area development in apple tree canopies. *Journal of Horticultural Science and Biotechnology, 81*(4), 575-582.

ROBINSON, T. L., & LAKSO, A. N. (2004). Between Year and Within Year Variation in Chemical Fruit Thinning Efficacy of Apple during Cool Springs. *Acta Horticulturae, 636*, 283-294.

ROBINSON, T. L., & LAKSO, A. N. (2011). Predicting Chemical Thinner Response with a Carbohydrate Model. *Acta Horticulturae, 903*, 743-750.

ROM, C. R., & BARRITT, B. (1990). Spur Development of `Delicious' Apple as Influenced by Position, Wood Age, Strain, and Pruning. *HortScience, 25*(12), 1578-1581.

ROUPSARD, O., DAUZAT, J., NOUVELLON, Y., DEVEAU, A., FEINTRENIE, L., SAINT-ANDRÉ, L., et al. (2008). Cross-validating Sun-shade and 3D models of light absorption by a tree-crop canopy. *Agricultural and Forest Meteorology, 148*(4), 549-564.

RUIZ-SÁNCHEZ, M. C., DOMINGO, R., & CASTEL, J. R. (2010). Review. Deficit irrigation in fruit trees and vines in Spain. *Spanish Journal of Agricultural Research, 8*, 5-20.

SCHOLANDER, P. F., HAMMEL, H. T., BRADSTREET, E. D., & HEMMINGSEN, E. A. (1965). Sap Pressure in Vascular Plants. *Science, 148*, 339-346.

SCHRADER, L., ZHANG, J., & SUN, J. (2003). Environmental Stresses that Cause Sunburn of Apple. *Acta Horticulturae, 618*, 397-405.

SCHRÖDER, M., & BANGERTH, F. (2006). The Possible 'Mode of Action' of Thinning Bioregulators and its Possible Contribution to the Understanding of 'Thinning Variability' in Apples. *Acta Horticulturae, 727*, 437-444.

SCHRÖDER, M., LINK, H., & BANGERTH, K. F. (2013). Correlative polar auxin transport to explain the thinning mode of action of benzyladenine on apple. *Scientia Horticulturae, 153*, 84-92.

SCHUPP, J. R., BAUGHER, T. A., MILLER, S. S., HARSH, R. M., & LESSER, K. M. (2008). Mechanical Thinning of Peach and Apple Trees Reduces Labor Input and Increases Fruit Size. *HortTechnology, 18*(4), 660-670.

SCHWEIZER, S., NEUMANN, L., BRAUN, P., KUTTNIG, S., BAUMGARTNER, D. G., & WIDMER, A. (2014). Behangsprognose bei Äpfeln. *Agrarforschung Schweiz, 5*(10), 422-429.

SEEM, R. C., ELFVING, D. C., OREN, T. R., & EISENSMITH, S. P. (1986). A carbon ballance model for apple tree growth and production. *Acta Horticulturae, 184*, 129-137.

SHACKEL, K., LAMPINEN, B., SIBBETT, S., & OLSON, W. (2000). The relation of midday stem water potential to the growth and physiology of fruit trees under water limited conditions. *Acta Horticulturae, 537*, 425-430.

SHACKEL, K. A., AHMADI, H., BIASI, W., BUCHNER, R., GOLDHAMER, D., GURUSINGHE, S., et al. (1997). Plant Water Status as an Index of Irrigation Need in Deciduous Fruit Trees. *HortTechnology, 7*(1), 23-29.

SINOQUET, H., LE ROUX, X., ADAM, B., AMÉGLIO, T., & DAUDET, F. A. (2001). RATP: a model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: application to an isolated tree crown. *Plant, Cell and Environment, 24*, 395-406.

SINOQUET, H., SONOHAT, G., POTEL, A.-M., MONNEY, P., & LAURI, P.-E. (2008). Using Virtual Plants to Estimate Light Distribution at Intra-Canopy Scale in Apple Trees: Method Presentation and Assessment. *Acta Horticulturae, 803*, 225-234.

SIRCELJ, H., TAUSZ, M., GRILL, D., & BATIC, F. (2007). Detecting different levels of drought stress in apple trees (*Malus domestica* Borkh.) with selected biochemical and physiological parameters. *Scientia Horticulturae, 113*(4), 362-369.

SMITH, W. H. (1950). Cell-multiplication and Cell-enlargement in the Development of the Flesh of the Apple Fruit. *Annals of Botany, 14*(53), 23-38.

SOKALSKA, D. I., HAMAN, D. Z., SZEWCZUK, A., SOBOTA, J., & DEREN, D. (2009). Spatial root distribution of mature apple trees under drip irrigation system. *Agricultural Water Management, 96*(6), 917-924.

SOLOMAKHIN, A., & BLANKE, M. M. (2010). Mechanical flower thinning improves the fruit quality of apples. *Journal of the Science of Food and Agriculture, 90*(5), 735-741.

SPITTERS, C. J. T., TOUSSAINT, H. A. J. M., & GOUDRIAAN, J. (1986). Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis Part I. Components of incoming radiation. *Agricultural and Forest Meteorology, 38*(1-3), 217-229.

SRITHARAN, R., & LENZ, F. (1989). The Influence of Long-Term Water Stress and Fruiting on Photosynthesis and Transpiration in Apple. *Gartenbauwissenschaft, 54*(4), 150-154.

STANLEY, C. J., TUSTIN, D. S., LUPTON, G., MCARTNEY, S., CASHMORE, W. M., & DE SILVA, H. N. (2000). Towards understanding the role of temperature in apple fruit growth responses in three geographical regions within New Zealand. *Journal of Horticultural Science & Biotechnology, 75*(4), 413-422.

STATISTA. (2011). Sortenanteile von Äpfeln in der EU in den Jahren 2007 bis 2011. Retrieved 24.03.2014, from http://de.statista.com/statistik/daten/studie/29114/umfrage/bedeutende-apfelsorten-in-der-eu-nach-sortenanteil/

STEPPE, K., DE PAUW, D. J. W., & LEMEUR, R. (2008). A step towards new irrigation scheduling strategies using plant-based measurements and mathematical modelling. *Irrigation Science, 26*, 505-517.

STEPPE, K., DE PAUW, D. J. W., LEMEUR, R., & VANROLLEGHEM, P. A. (2006). A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree Physiology, 26*(3), 257-273.

STÖCKLE, C. O., MARSAL, J., & VILLAR, J. M. (2011). Impact of Climate Change on Irrigated Tree Fruit Production. *Acta Horticulturae, 889*, 41-52.

STREIF, J. (1989). Erfahrungen mit Erntetermin-Untersuchungen bei Äpfeln. *Besseres Obst, 34*, 235-238.

TALLUTO, G., FARINA, V., VOLPE, G., & LO BIANCO, R. (2008). Effects of partial rootzone drying and rootstock vigour on growth and fruit quality of 'Pink Lady' apple trees in Mediterranean environments. *Australian Journal of Agricultural Research, 59*, 785-794.

TIMLIN, D., BUNCE, J., FLEISHER, D., REDDY, V. R., YANG, Y., KIM, S.-H., et al. (2008). Simulation of the Effects of Limited Water on Photosynthesis and Transpiration in Field Crops: Can We Advance Our Modeling Approaches? In L. R. Ahuja, V. R. Reddy, S. A. Saseendran & Q. Yu (Eds.), *Response of Crops to Limited Water - Understanding and Modeling Water Stress Effects on Plant Growth Processes*. Madison: ASA, CSSA, SSSA.

TOJNKO, S., & CMELIK, Z. (2004). Influence of Irrigation and Fertilization on Performances of Young Apple Trees. *Acta Horticulturae, 664*, 661-663.

TROMP, J. (2000). Flower-bud formation in pome fruits as affected by fruit thinning. *Plant Growth Regulation, 31*(1), 27-34.

TROMP, J. (2005). Metabolic processes. In J. Tromp, A. Webster & S. J. Wertheim (Eds.), *Fundamentals of Temperate Zone Tree Fruit Production* (pp. 39-54). Leiden, The Netherlands: Backhuys Publishers.

TROMP, J., & WERTHEIM, S. J. (2005). Fruit growth and development. In J. Tromp, A. Webster & S. J. Wertheim (Eds.), *Fundamentals of Temperate Zone Tree Fruit Production* (pp. 240-266). Leiden: Backhuys Publishers.

VALANCOGNE, C., DAYAU, S., AMEGLIO, T., ARCHER, P., DAUDET, F. A., FERREIRA GAMA, M. I., et al. (1997). Relations between relative transpiration and predawn leaf water potential in different fruit tree species. *Acta Horticulturae, 449*, 423-429.

VAN LEEUWEN, C., TREGOAT, O., CHONÉ, X., BOIS, B., PERNET, D., & GAUDILLÈRE, J. P. (2009). Vine water status is a key factor in grape ripening and vintage quality for red Bordeaux wine. *Journal International des Sciences de la Vigne et du Vin, 43*, 121-134.

VIRGINIA STATE UNIVERSITY. (2014). MaluSim Carbohydrate Model. Retrieved 26.05.2014, 2014, from http://blogs.ext.vt.edu/tree-fruit-horticulture/; http://blogs.ext.vt.edu/tree-fruit-horticulture/2012/05/10/malusim-carbohydrate-model-for-may-10/

VOS, J., EVERS, J. B., BUCK-SORLIN, G. H., ANDRIEU, B., CHELLE, M., & DE VISSER, P. H. B. (2010). Functional–structural plant modelling: a new versatile tool in crop science. *Journal of Experimental Botany, 61*(8), 2101-2115.

WANG, Y. P., & LEUNING, R. (1998). A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I:: Model description and comparison with a multi-layered model. *Agricultural and Forest Meteorology, 91*(1-2), 89-111.

WANG, Z., QUEBEDEAUX, B., & STUTTE, G. W. (1995). Osmotic Adjustment: Effect of Water Stress on Carbohydrates in Leaves, Stems and Roots of Apple. *Australian Journal of Plant Physiology, 22*, 747-754.

WANG, Z., & STUTTE, G. W. (1992). The Role of Carbohydrates in Active Osmotic Adjustment in Apple under Water Stress. *Journal of the American Society for Horticultural Science, 117*(5), 816-823.

WARRINGTON, I. J., FULTON, T. A., HALLIGAN, E. A., & DE SILVA, H. N. (1999). Apple Fruit Growth and Maturity are Affected by Early Season Temperatures. *Journal of the American Society for Horticultural Science, 124*(5), 468-477.

WATSON, R. L., LANDSBERG, J. J., & THORPE, M. R. (1978). Photosynthetic characteristics of the leaves of ‘Golden Delicious’ appletrees. *Plant, cell & environment, 1*(1), 51-58.

WERTHEIM, S. J. (2000). Developments in the chemical thinning of apple and pear. *Plant Growth Regulation, 31*, 85-100.

WERTHEIM, S. J., & SCHMIDT, H. (2005). 17 Flowering, pollination and fruit set. In J. Tromp, A. Webster & S. J. Wertheim (Eds.), *Fundamentals of Temperate Zone Tree Fruit Production* (pp. 216-239). Leiden: Backhuys Publishers.

WERTHEIM, S. J., & WEBSTER, A. D. (2005). 19 Manipulation of growth and development by plant bioregulators. In J. Tromp, A. D. Webster & S. J. Wertheim (Eds.), *Fundamentals of Temperate Zone Tree Fruit Production* (pp. 267-294). Leiden: Backhuys Publishers, Leiden, The Netherlands.

WIBBE, M. L., & BLANKE, M. M. (1997). Effect of fruiting and drought or flooding on carbon balance of apple trees. *Photosynthetica, 33*(2), 269-275.

WIBBE, M. L., BLANKE, M. M., & LENZ, F. (1994). Respiration of apple trees between leaf fall and leaf emergence. *Environmental and Experimental Botany, 34*(1), 25-30.

WILLAUME, M., LAURI, P.-E., & SINOQUET, H. (2004). Light interception in apple trees influenced by canopy architecture manipulation. *Trees, 18*, 705-713.

WÜNSCHE, J. N., GREER, D. H., LAING, W. A., & PALMER, J. W. (2005). Physiological and biochemical leaf and tree responses to crop load in apple. *Tree Physiology, 25*, 1253-1263.

WÜNSCHE, J. N., & LAKSO, A. N. (2000). The Relationship Between Leaf Area and Light Interception by Spur and Extension Shoot Leaves and Apple Orchard Productivity. *HortScience, 35*(7), 1202-1206.

WÜNSCHE, J. N., LAKSO, A. N., & ROBINSON, T. L. (1995). Comparison of Four Methods for Estimating Total Light Interception by Apple Trees of Varying Forms. *HortScience, 30*(2), 272-276.

WÜNSCHE, J. N., LAKSO, A. N., ROBINSON, T. L., LENZ, F., & DENNING, S. S. (1996). The Bases of Productivity in Apple Production Systems: The Role of Light Interception by Different Shoot Types. *Journal of the American Society of Horticultural Sciences, 121*(5), 886-893.

WÜNSCHE, J. N., PALMER, J., & GREER, D. H. (2000). Effects of Crop Load on Fruiting and Gas-exchange Chraracteristics of 'Braeburn'/M.26 Apple Trees at Full Canopy. *Journal of the American Society of Horticultural Sciences, 125*(1), 93-99.

YUAN, R., & GREENE, D. W. (2000). Benzyladenine as A Chemical Thinner for 'McIntosh' Apples. I. Fruit Thinning Effects and Associated Relationships with Photosynthesis, Assimilate Translocation, and Nonstructural Carbohydrates. *Journal of the American Society for Horticultural Science, 125*(2), 169-176.

YURI, J. A., TALICE, J. G., VERDUGO, J., & DEL POZO, A. (2011). Responses of fruit growth, quality, and productivity to crop load in apple cv. Ultra Red Gala/MM111. *Scientia Horticulturae, 127*(3), 305-312.

ZEBISCH, M., GROTHMANN, T., SCHRÖTER, D., HASSE, C., FRITSCH, U., & CRAMER, W. (2005). *Climate Change in Germany*. Potsdam Institute for Climate Impact Research; Commissioned by the Federal Environmental Agency (UBA), Germany

ZEGBE, J. A., & SERNA-PÉREZ, A. (2011). Partial rootzone drying maintains fruit quality of 'Golden Delicious' apples at harvest and postharvest. *Scientia Horticulturae, 127*, 455-459.

ZHANG, S. Y., ZHANG, G. C., GU, S. Y., XIA, J. B., & ZHAO, J. K. (2010). Critical responses of photosynthetic efficiency of goldspur apple tree to soil water variation in semiarid loess hilly area. *Photosynthetica, 48*(4), 589-595.

ZHAO, J. Y., WANG, L. J., FAN, P. G., DAI, Z. W., & HUA LI, S. (2006). Effect of Half and Whole Root Drying on Photosynthesis, Nitrate Concentration, and Nitrate Reductase Activity in Roots and Leaves of Micropropagated Apple Plants. *Journal of the American Society for Horticultural Science, 131*(6), 709-715.

ZHOU, R., & QUEBEDEAUX, B. (2003). Changes in Photosynthesis and Carbohydrate Metabolism in Mature Apple Leaves in Response to Whole Plant Source-Sink Manipulation. *Journal of the American Society of Horticultural Science, 128*(1), 113-119.

ZHOU, R., SICHER, R., & QUEBEDEAUX, B. (2001). Diurnal changes in carbohydrate metabolism in mature apple leaves. *Australian Journal of Plant Physiology, 28*, 1143-1150.

ZIBORDI, M., DOMINGOS, S., & CORELLI-GRAPPADELLI, L. (2009). Thinning apples via shading: an appraisal under field conditions. *Journal of Horticultural Science and Biotechnology, ISAFRUIT Special Issue*, 138-144.

ZWEIFEL, R., ITEM, H., & HÄSLER, R. (2001). Link between diurnal stem radius changes and tree water relations. *Tree Physiology, 21*(12-13), 869-877.

10 APPENDIX

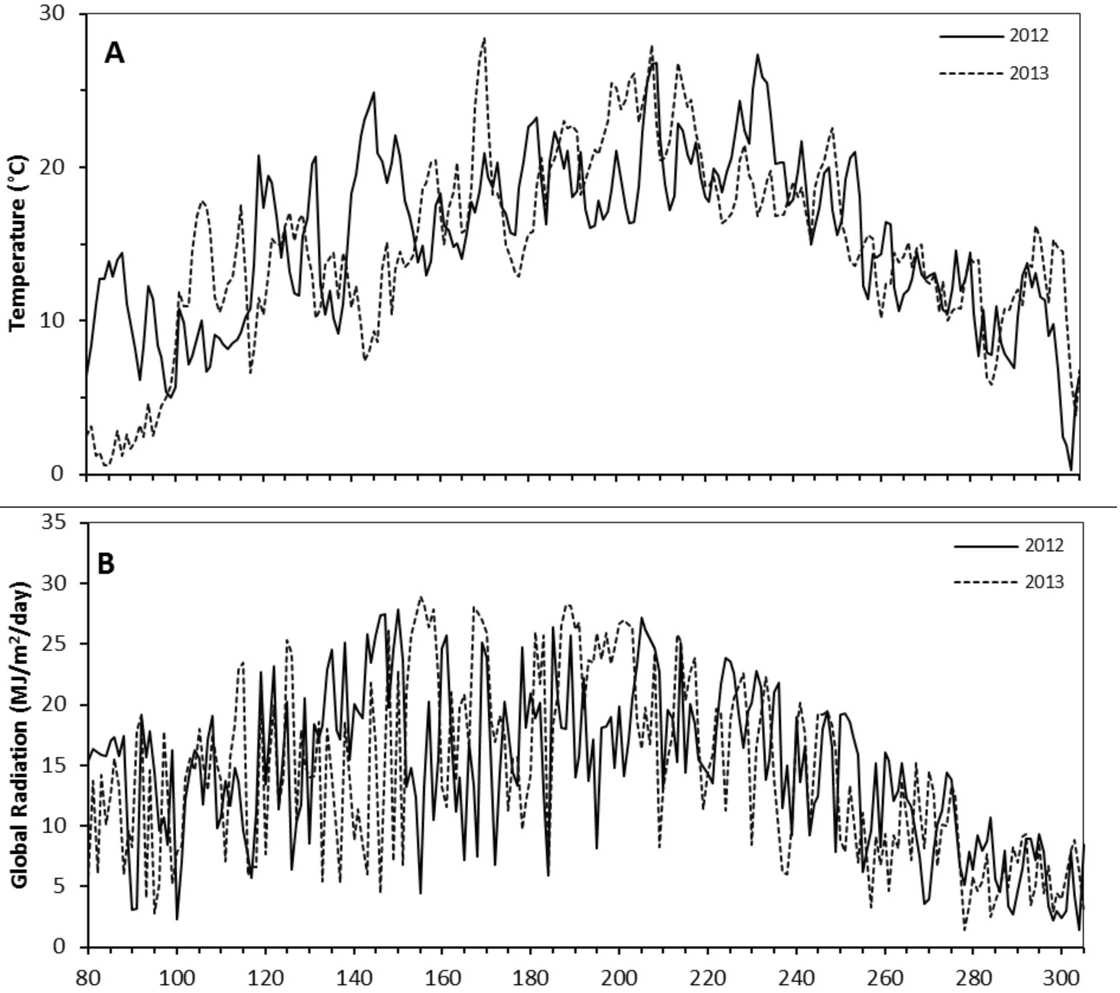

Figure 26: Mean temperature (A) and global radiation (B) for 2012 (solid black line) and 2013 (dashed black line) from DOY 80 to 305.

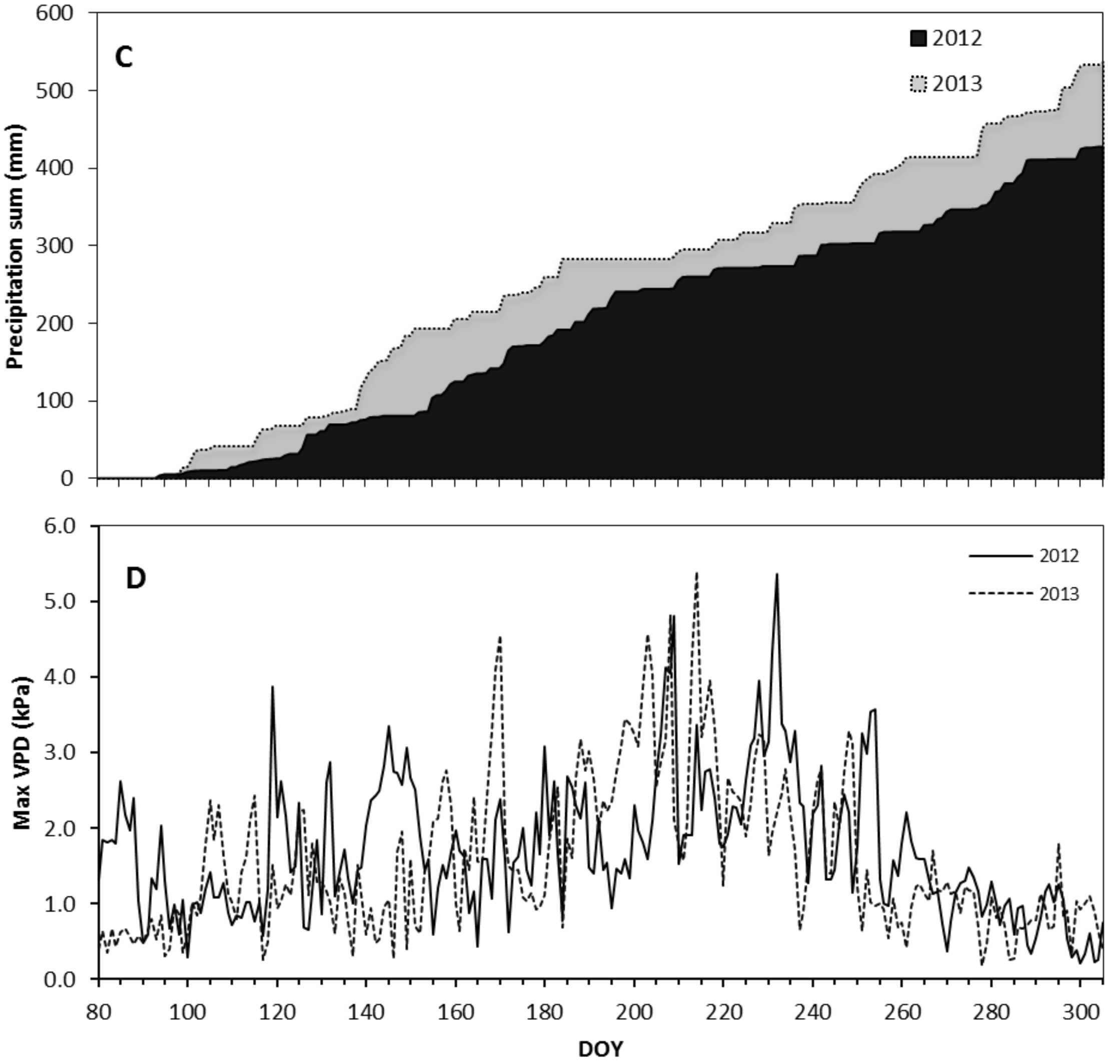

Figure 27: Accumulated precipitation (C) and maximum VPD (D) for 2012 (solid black line) and 2013 (dashed black line/grey), from DOY 80 to 305.

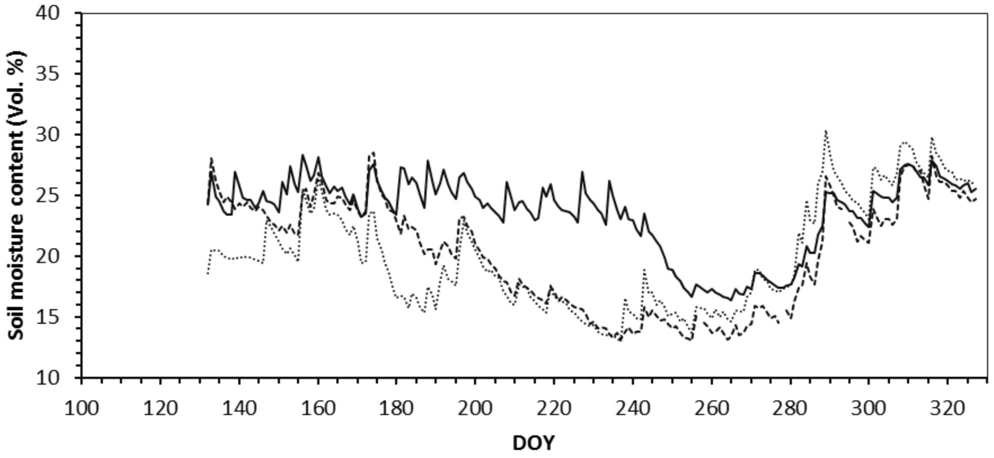

Figure 28: Soil moisture content from 0 to 30 cm depth measured with TDR probes in 2012 for CT (dotted line), NT (dashed line), and ET (solid line).

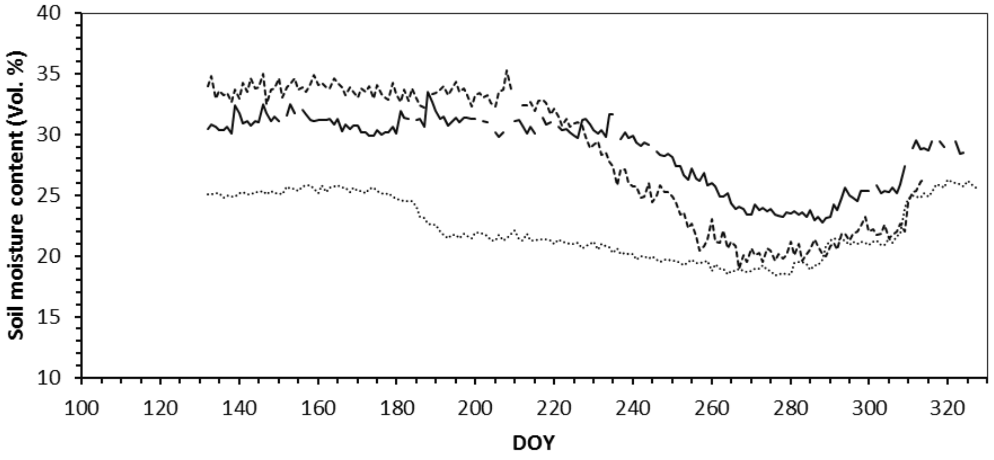

Figure 29: Soil moisture content from 30 to 60 cm depth measured with TDR probes in 2012 for CT (dotted line), NT (dashed line), and ET (solid line).

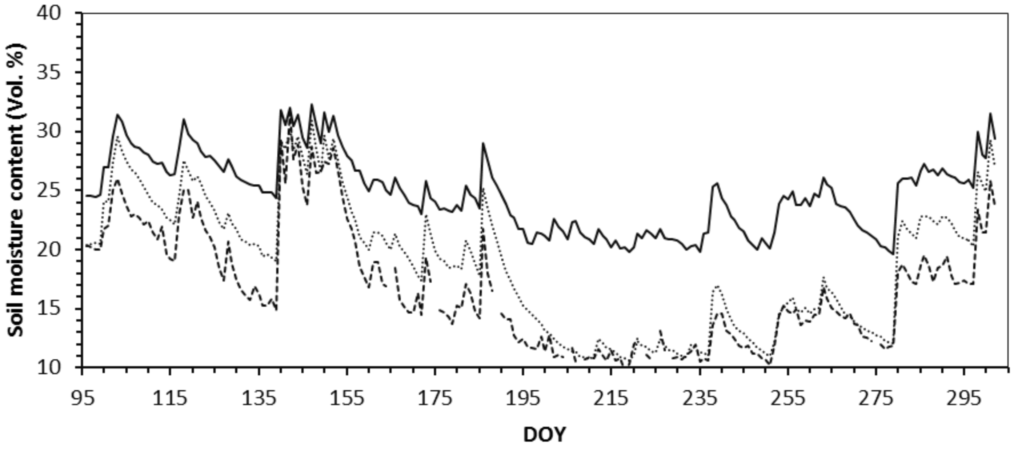

Figure 30: Soil moisture content from 0 to 30 cm depth measured with TDR sensors in 2013 for CT (dotted line), NT (dashed line), and ET (solid line).

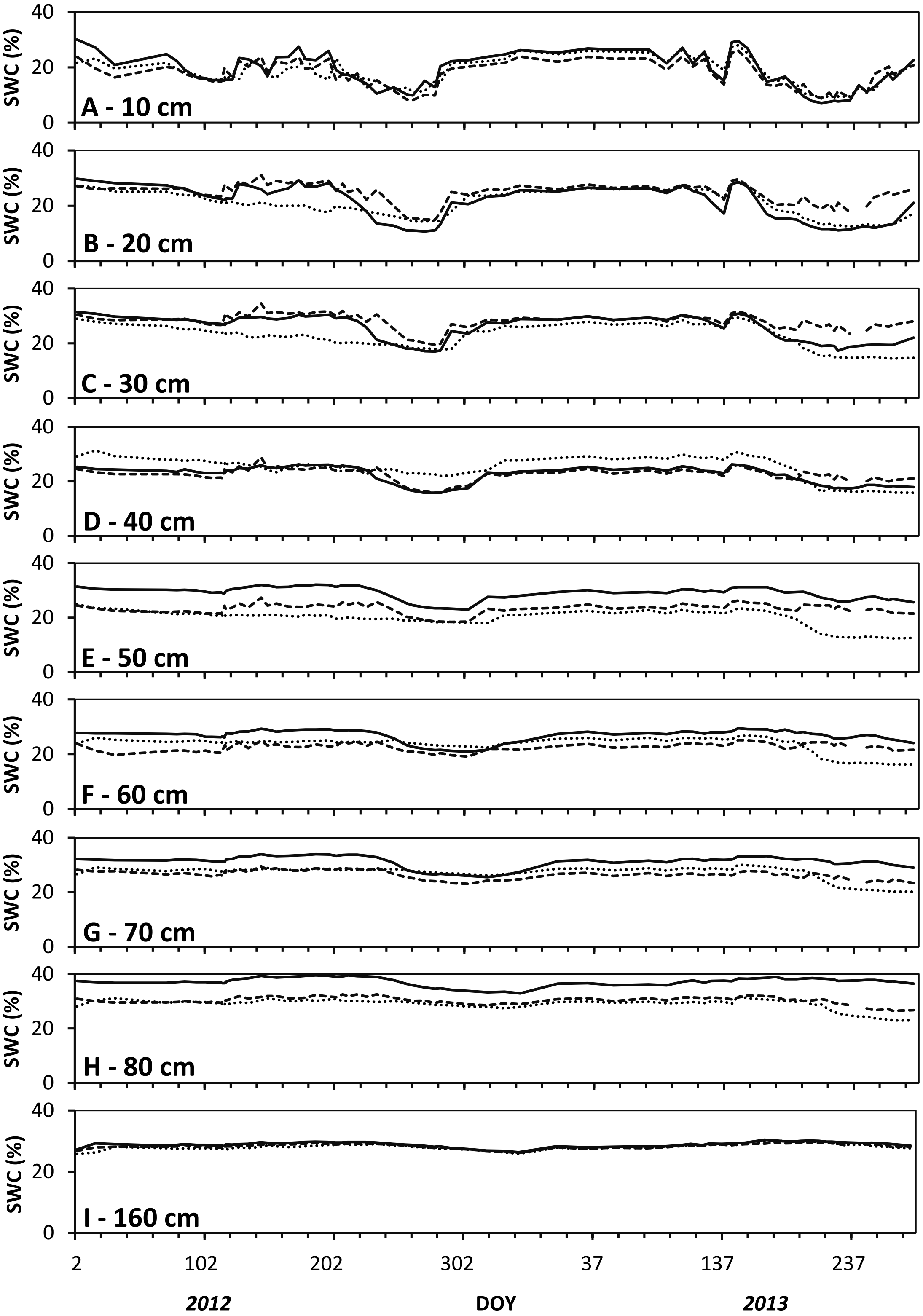

Figure 31: Diviner 2000 soil water content (SWC) measurements in 10 cm (A), 20 cm (B), 30 cm (C), 40 cm (D), 50 cm (E), 60 cm (F), 70 cm (G), 80 cm (H), and 160 cm (I) depth for CT (dotted line), ET (dashed line) and NT(solid line), 2012-2013.

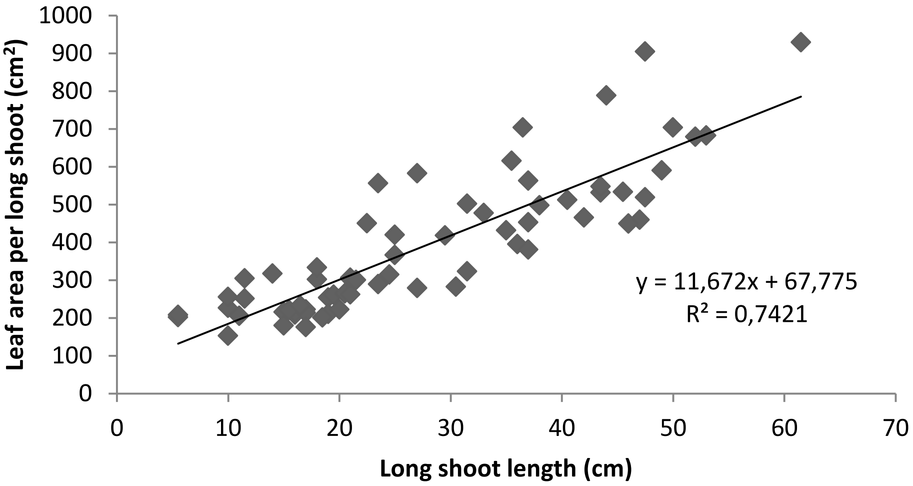

Figure 32: Relationship between overall long shoot length and leaf area obtained for 'Wellant'.

Table 22: Mean predawn water potential values and standard deviations (n=3) of CT, NT, and ET of 'Wellant' for all measurement days in 2012. Mean values followed by a different letter in each column are significantly different at $p \leq 0.05$, tested by one-way ANOVA with post-hoc Tukey's HSD test. On DOY 200 homogeneity of variances between groups was negative and therefore Games Howell post-hoc test has been used.

DOY	171	178	185	193	200	206	214
Var.\Date	06/19/2012	06/26/2012	07/03/2012	07/11/2012	07/18/2012	07/24/2012	08/01/2012
CT	-0.26 ± 0.04 a	-0.13 ± 0.03 a	-0.12 ± 0.03 a	-0.12 ± 0.03 a	-0.09 ± 0.01 a'	-0.20 ± 0.02 a	-0.17 ± 0.01 a
NT	-0.08 ± 0.02 b	-0.08 ± 0.06 a	-0.05 ± 0.01 b	-0.08 ± 0.01 ab	-0.05 ± 0.00 b'	-0.08 ± 0.01 b	-0.09 ± 0.01 b
ET	-0.17 ± 0.04 c	-0.08 ± 0.03 a	-0.03 ± 0.01 b	-0.07 ± 0.02 b	-0.06 ± 0.02 ab'	-0.14 ± 0.04 a	-0.10 ± 0.01 b

DOY	221	228	235	249	255	262
Var.\Date	08/08/2012	08/15/2012	08/22/2012	09/05/2012	09/11/2012	09/18/2012
CT	-0.20 ± 0.03 a	-0.36 ± 0.01 a	-0.40 ± 0.02 a	-0.35 ± 0.08 a	-0.56 ± 0.06 a	-0.28 ± 0.02 a
NT	-0.11 ± 0.01 b	-0.24 ± 0.01 b	-0.12 ± 0.02 b	-0.14 ± 0.02 b	-0.43 ± 0.05 b	-0.15 ± 0.01 b
ET	-0.09 ± 0.01 b	-0.20 ± 0.02 c	-0.15 ± 0.01 b	-0.19 ± 0.06 b	-0.34 ± 0.04 b	-0.11 ± 0.03 b

Table 23: Mean midday stem water potential values and standard deviations (n=3) of CT, NT, and ET of 'Wellant' for all measurement days in 2012. Mean values followed by a different letter in each column are significantly different at $p \leq 0.05$, tested by one-way ANOVA with post-hoc Tukey's HSD test.

DOY	166	170	171	178	180	185	193
Var.\Date	06/14/2012	06/18/2012	06/19/2012	06/26/2012	06/28/2012	07/03/2012	07/11/2012
CT	-0.77 ± 0.06 a	-1.7 ± 0.02 a	-1.69 ± 0.19 a	-1.64 ± 0.12 a	-2.02 ± 0.35 a	-1.86 ± 0.06 a	-1.28 ± 0.02 a
NT	-0.88 ± 0.03 b	-1.18 ± 0.09 b	-1.04 ± 0.03 b	-0.8 ± 0.06 b	-1.6 ± 0.22 a	-1.39 ± 0.11 b	-0.88 ± 0.01 b
ET	-0.82 ± 0.02 ab	-1.6 ± 0.03 a	-1.52 ± 0.24 a	-1.35 ± 0.09 c	-1.28 ± 0.04 a	-1.51 ± 0.17 b	-1.06 ± 0.10 c

DOY	200	205	206	208	213	215	221
Var.\Date	07/18/2012	07/23/2012	07/24/2012	07/26/2012	07/31/2012	08/02/2012	08/08/2012
CT	-1.3 ± 0.07 a	-1.5 ± 0.05 a	-1.68 ± 0.17 a	-1.59 ± 0.06 a	-0.97 ± 0.06 a	-1.21 ± 0.12 a	-1.25 ± 0.17 a
NT	-0.91 ± 0.05 b	-0.83 ± 0.04 c	-1.06 ± 0.04 c	-1.18 ± 0.12 b	-0.54 ± 0.04 b	-0.72 ± 0.05 b	-0.84 ± 0.18 b
ET	-1.19 ± 0.09 a	-1.09 ± 0.13 b	-1.32 ± 0.03 b	-1.28 ± 0.03 b	-0.53 ± 0.03 b	-0.91 ± 0.01 c	-0.68 ± 0.03 b

DOY	227	228	235	250	254	261
Var.\Date	08/14/2012	08/15/2012	08/22/2012	09/06/2012	09/10/2012	09/17/2012
CT	-1.62 ± 0.30 a	-1.64 ± 0.17 a	-1.85 ± 0.32 a	-1.48 ± 0.32 a	-1.74 ± 0.14 a	-1.26 ± 0.17 a
NT	-1.03 ± 0.10 b	-1.17 ± 0.07 b	-0.97 ± 0.05 b	-1.1 ± 0.17 a	-1.43 ± 0.16 a	-1.16 ± 0.01 a
ET	-0.75 ± 0.06 b	-0.85 ± 0.03 c	-0.85 ± 0.05 b	-1.12 ± 0.07 a	-1.45 ± 0.11 a	-1.13 ± 0.13 a

Table 24: Average values of leaf photosynthetic rate with standard deviation for every measurement date for CT, NT, and ET in 2012. Mean values (n=3-12, depending on weather conditions on the specific measurement day; n is similar for all treatments for one specific measurement day and measurements were performed at a similar time of day) followed by a different letter in each column are significantly different at $p \leq 0.05$.

DOY	170	171	178	180	185	193	200
Var.\Date	06/18/2012	06/19/2012	06/26/2012	06/28/2012	07/03/2012	07/11/2012	07/18/2012
CT	18.4 ± 2.15 a	14.2 ± 2.11 a	14.5 ± 3.33 a	5.5 ± 2.27 a	10 ± 5.15 a	15.6 ± 0.88 a	11.3 ± 2.08 a
NT	16.9 ± 1.97 a	18.4 ± 2.29 b	11 ± 2.38 b	7.8 ± 2.38 a	12.7 ± 4.94 a	19.1 ± 1.22 b	14.6 ± 1.48 b
ET	16.1 ± 2.97 a	13.4 ± 2.34 a	14.3 ± 4.70 ab	7 ± 2.06 a	13.1 ± 5.10 a		12.8 ± 2.54 ab

DOY	205	206	208	213	221	222	227
Var.\Date	07/23/2012	07/24/2012	07/26/2012	07/31/2012	08/08/2012	08/09/2012	08/14/2012
CT	7.8 ± 1.55 a	5.8 ± 2.97 a	6 ± 2.25 a	13.4 ± 2.44 a	10.7 ± 1.23 a	10.5 ± 0.41 a	8.6 ± 2.52 a
NT	13.6 ± 3.49 b	11.7 ± 2.01 b	12 ± 2.39 b	17.6 ± 1.61 b	15.3 ± 1.94 b	14.7 ± 2.49 a	11.5 ± 2.90 a
ET	12.9 ± 1.65 b	10.2 ± 2.91 b	12.2 ± 1.39 b	16 ± 3.58 ab		14.6 ± 3.88 a	12.1 ± 2.53 a

DOY	236	250	254	261
Var.\Date	08/23/2012	09/06/2012	09/10/2012	09/17/2012
CT	6.4 ± 1.46 a	10.4 ± 1.63 a	8.1 ± 1.18 a	12.8 ± 3.09 a
NT	9.9 ± 3.72 a	14.7 ± 3.04 b	10 ± 3.39 a	14.6 ± 5.28 a
ET	13.6 ± 3.76 a	15.5 ± 1.78 b	10.3 ± 3.02 a	12.9 ± 2.63 a

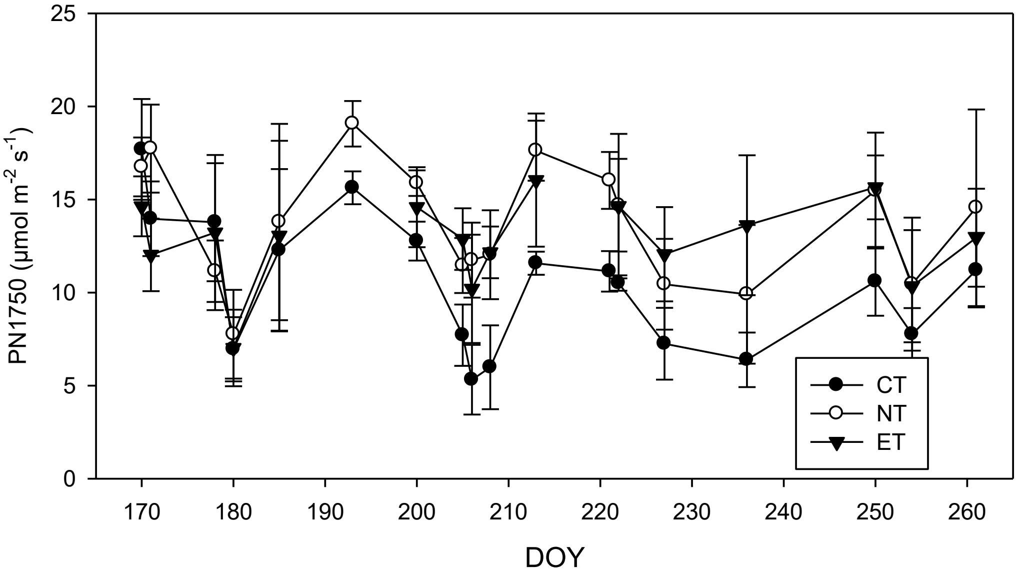

Figure 33: PN1750 measured between 11 a.m. and 3 p.m. in 2012 for CT, NT, and ET of 'Wellant', error bars indicate standard deviations (n=3-9, depending on weather conditions on the specific measurement day; n is similar for all treatments for one specific measurement day and measurements were performed at a similar time of day).

Table 25: Average values of leaf photosynthetic rate with standard deviation for every measurement date for CT, NT, and ET of 'Wellant' in 2013. Mean values (n=3-9, depending on weather conditions on the specific measurement day; n is similar for all treatments for one specific measurement day and measurements were performed at a similar time of day) followed by a different letter in each column are significantly different at p ≤ 0.05.

DOY	148	156	168	177	198
Var.\Date	05/28/13	06/05/13	06/17/13	06/26/13	07/17/13
CT	-13.8 ± 1.50 a	-14.2 ± 1.53 a	-17.8 ± 2.48 a	-17.9 ± 0.86 a	-14.5 ± 1.70 a
ET	-14.3 ± 2.71 a	-15.2 ± 1.75 a	-18.4 ± 2.48 a	-17.8 ± 0.87 a	-15.9 ± 0.62 a
NT	-13.1 ± 1.23 a	-13.9 ± 1.55 a	-16.1 ± 3.05 a	-17.3 ± 1.06 a	-12.4 ± 2.12 a

DOY	200	212	218	225	241
Var.\Date	07/19/13	07/31/13	08/06/13	08/13/13	08/29/13
CT	-12.6 ± 3.66 a	-9.6 ± 4.71 a	-8.4 ± 5.22 a	-10.3 ± 4.35 a	-14.4 ± 2.42 a
ET	-13.2 ± 0.63 a	-17.5 ± 0.62 a	-17.1 ± 1.03 b	-19 ± 0.67 b	-19.3 ± 0.85 b
NT	-14.5 ± 3.26 a	-16.1 ± 1.69 a	-13.6 ± 1.84 ab	-15.6 ± 4.82 ab	-17.7 ± 0.85 ab

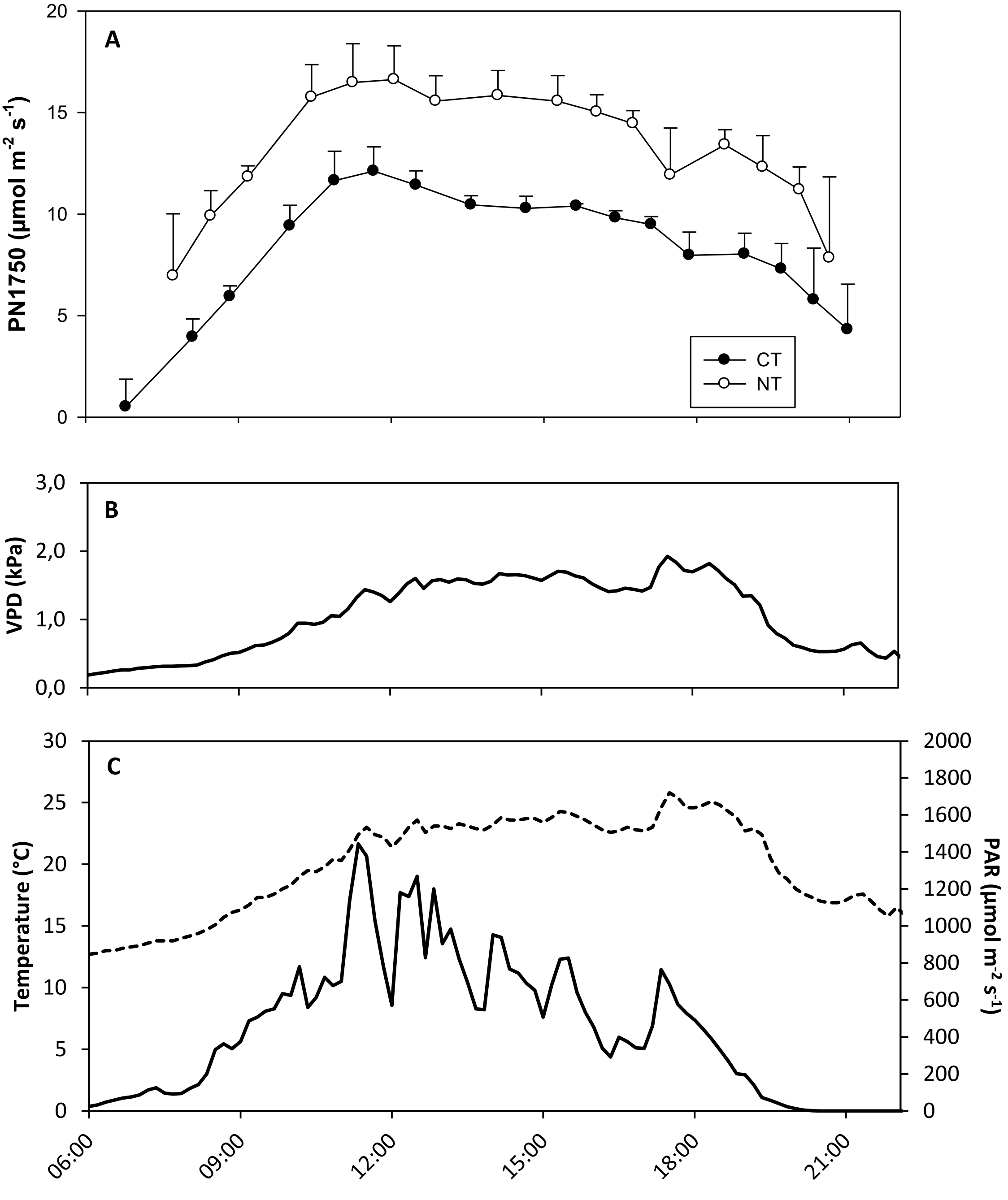

Figure 34: Daily course of PN1750 of CT and NT (A), error bars indicate standard deviations (n=3), vapor pressure deficit (B), temperature (dashed black line) and photosynthetic active radiation (solid black line) (C) on DOY 221 in 2012.

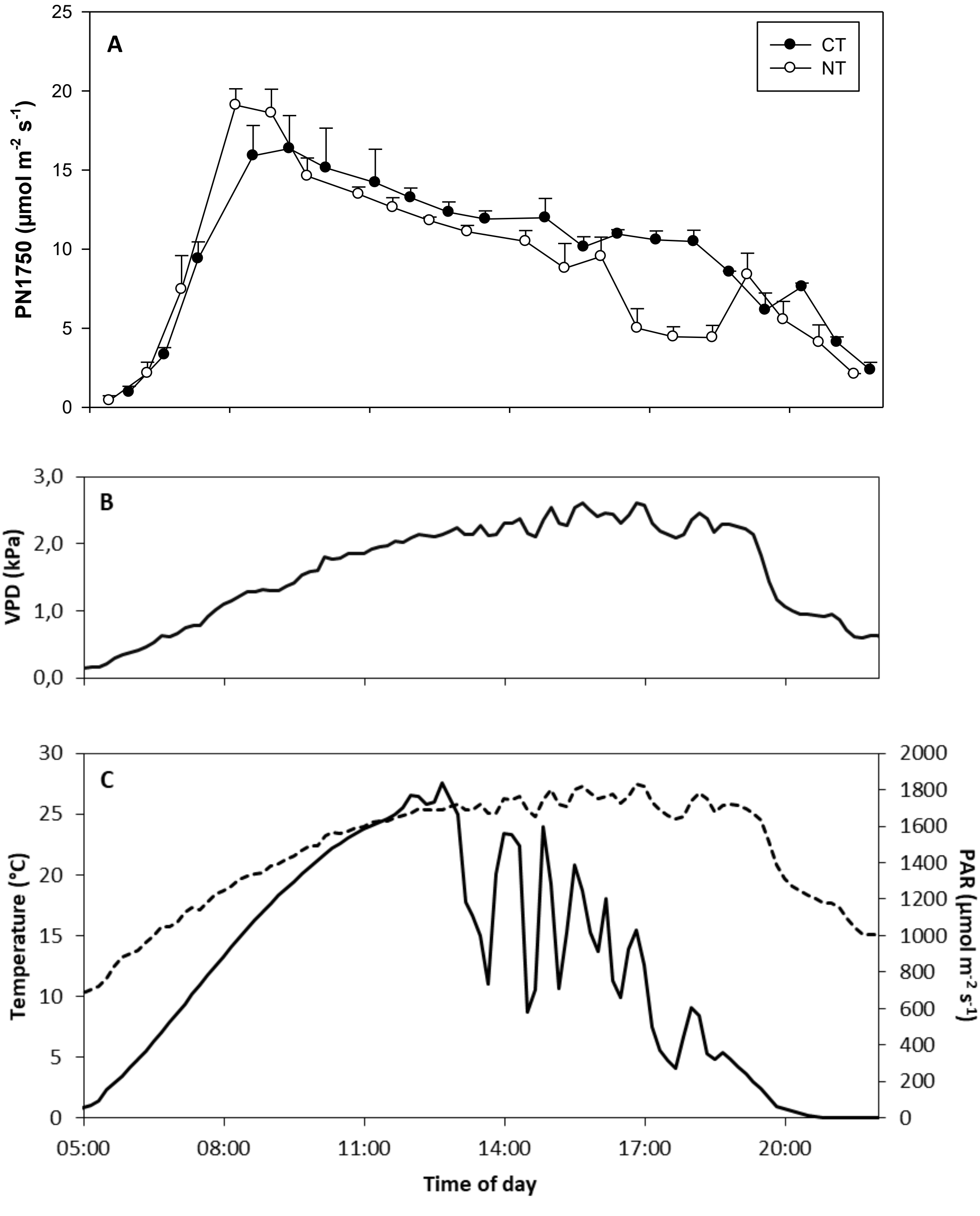

Figure 35: Daily course of PN1750 of CT and NT (A), error bars indicate standard deviations (n=3), vapor pressure deficit (B), temperature (dashed black line) and photosynthetic active radiation (solid black line) (C) on DOY 157 in 2013.

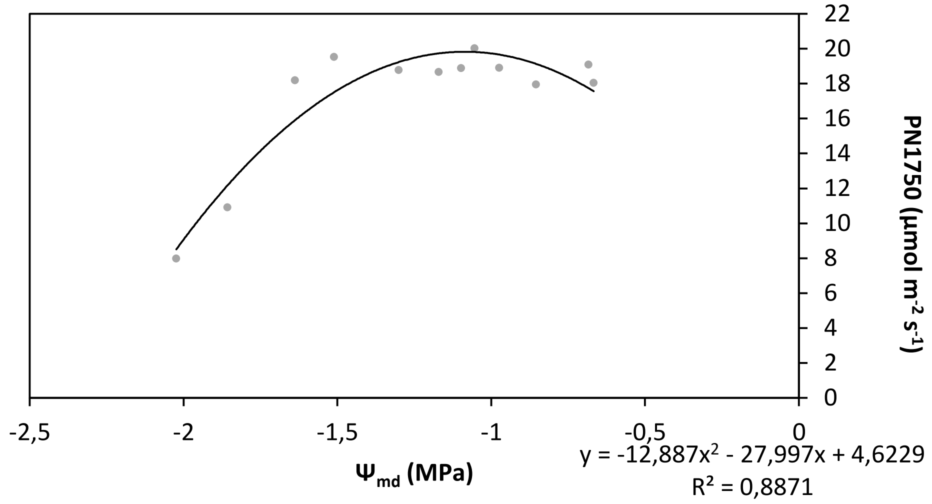

Figure 36: Selected high values of PN1750 measurements of 2012 and 2013 (12 to 4:30 p.m.) of Figure 17.

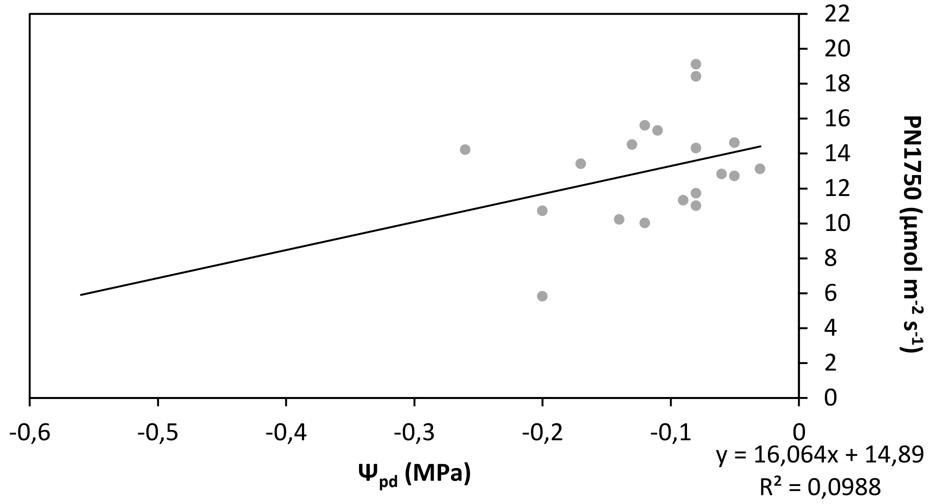

Figure 37: Average daily PN1750 and corresponding average daily Ψ_{pd} measurements (2012).

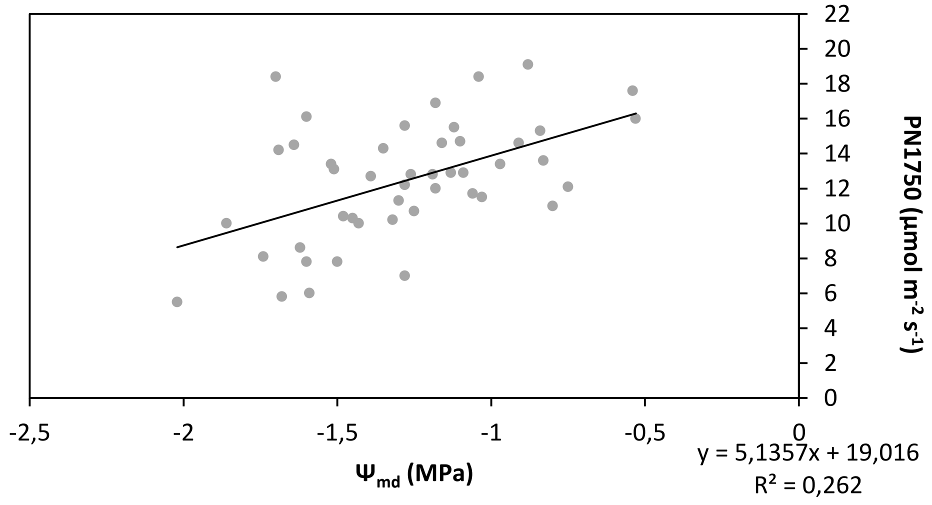

Figure 38: Average daily PN1750 and corresponding average daily Ψ_{md} measurements (2012).

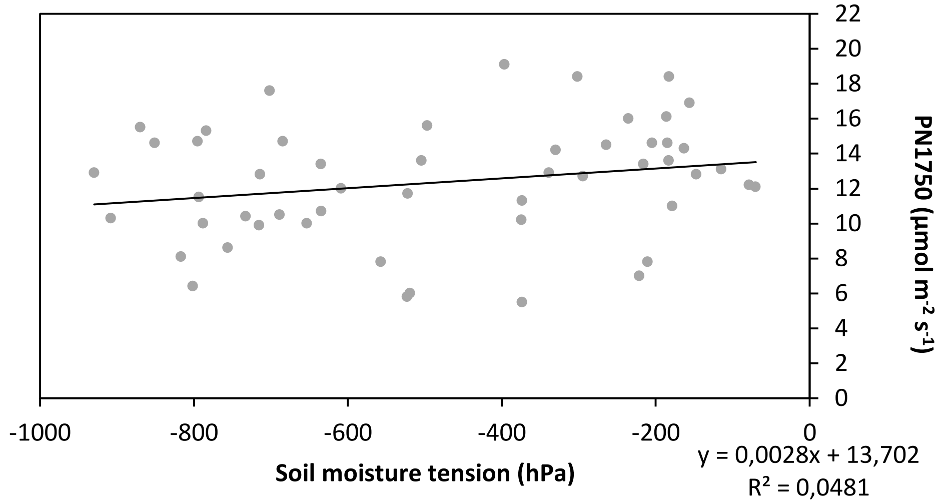

Figure 39: Average daily PN1750 and corresponding tensiometer measurements in 25 cm (2012).

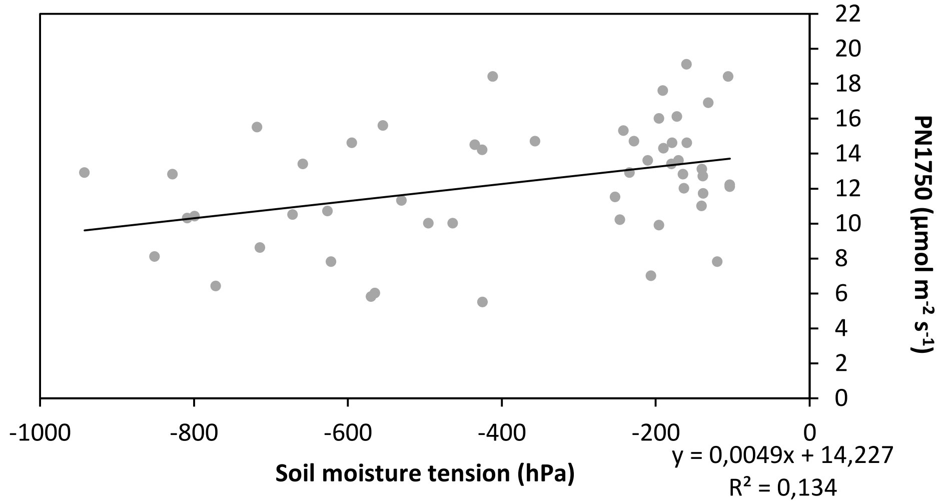

Figure 40: Average daily PN1750 and corresponding tensiometer measurements in 50 cm (2012).

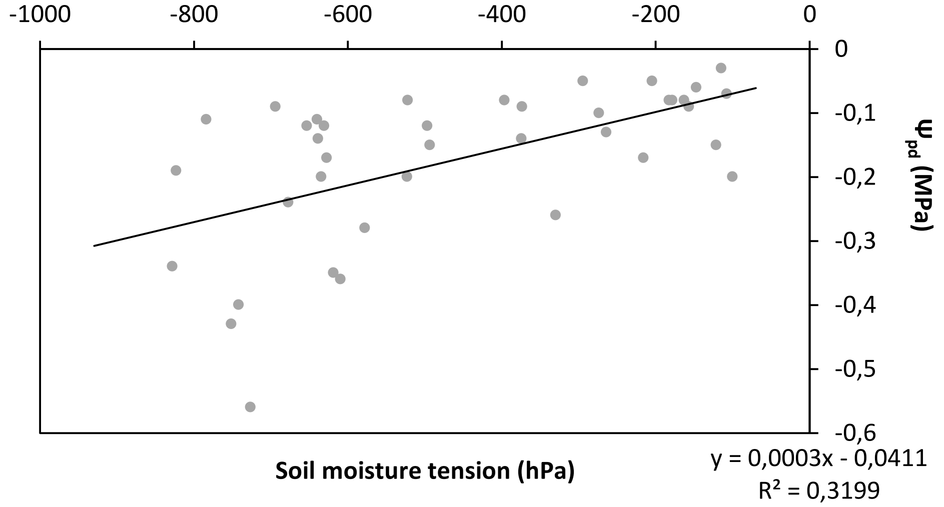

Figure 41: Average daily Ψ_{pd} and corresponding tensiometer measurements in 25 cm depth (2012).

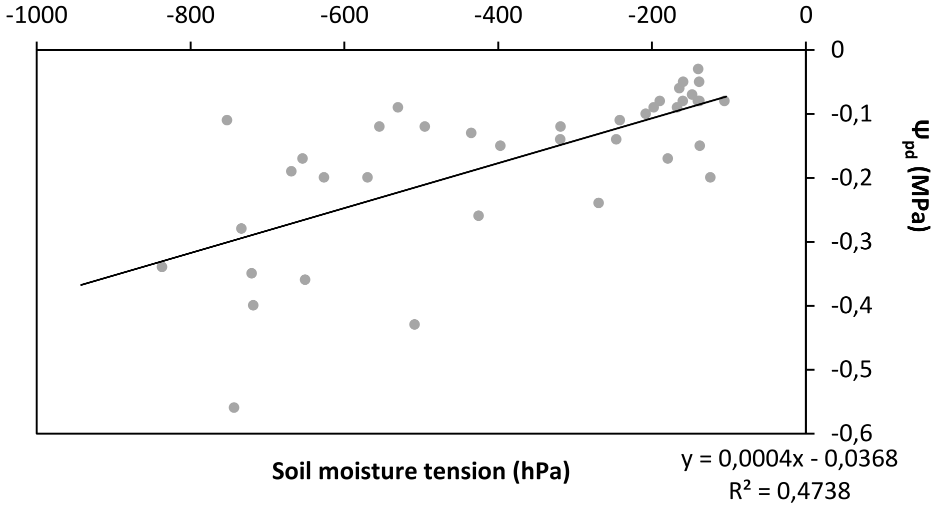

Figure 42: Average daily Ψ_{pd} and corresponding tensiometer measurements in 50 cm (2012).

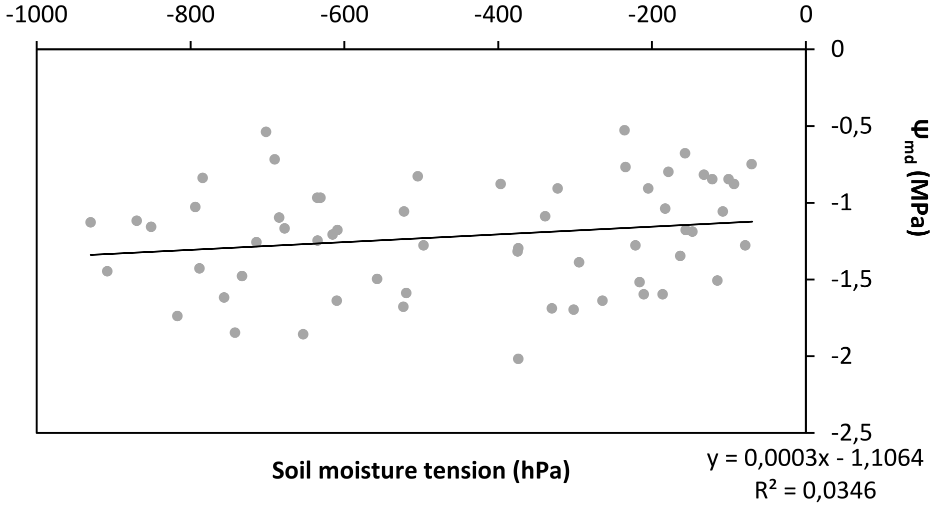

Figure 43: Average daily Ψ_{md} and corresponding tensiometer measurements in 25 cm (2012).

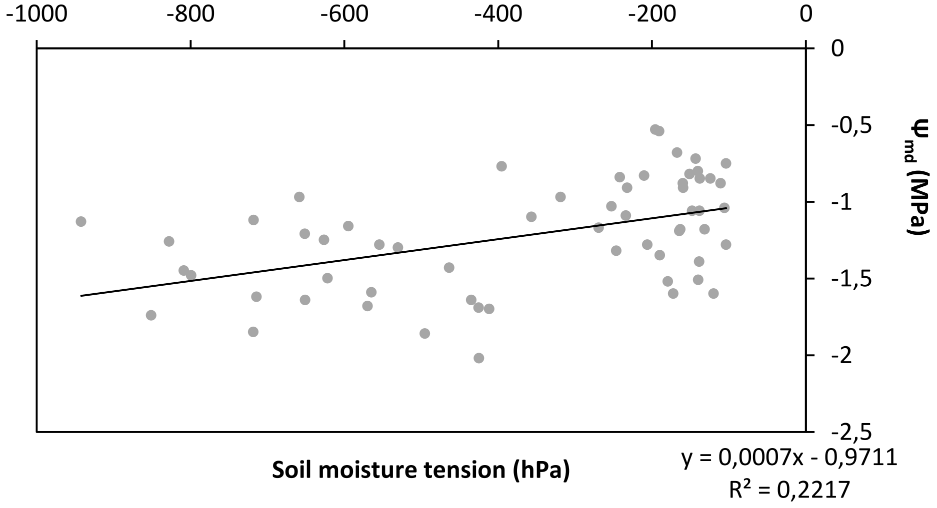

Figure 44: Average daily Ψ_{md} and corresponding tensiometer measurements in 50 cm depth (2012).

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Veröffentlichungen

Neumann, L., Braun, P. and Lakso, A.N. (2015). Adapting the MaluSim model to Mid-European growing systems. Acta Hortic. 1068, 221-226
https://doi.org/10.17660/ActaHortic.2015.1068.27
Basierend auf einem Vortrag beim *IX International Symposium on Modelling in Fruit Research and Orchard Management* in Montreal, Kanada im Juni 2011.

Neumann, L. and Braun, P. (2017). Effects of irrigation on development and photosynthesis of young apple trees. Acta Hortic. 1177, 265-272
https://doi.org/10.17660/ActaHortic.2017.1177.38
Basierend auf einem Vortrag beim *International Symposium on Physiological Principles and Their Application to Fruit Production* in Geneva, USA im März 2014.

Schweizer, S., **Neumann, L.,** Braun, P., Kuttnig, S., Baumgartner, D., & Widmer, A. (2014) Behangsprognose bei Äpfeln. Agrarforschung Schweiz 5 (10): 422–429
(Zusätzlich erschienen auf Französisch: ‚Prédiction de la charge des pommiers‘)

Schweizer S., Kuttnig S., Baumgartner D., Widmer A., **Neumann L.,** Braun P. (2014): Behangsprognose im Apfelbau. Obst und Weinbau 150 (18) S. 8 - 11.

Früchtenicht, E.; **Neumann, L.;** Klein, N.; Bonal, D.; Brüggemann, W (2018): Response of Quercus robur and two potential climate change winners - Quercus pubescens and Quercus ilex - to two years summer drought in a semi-controlled competition study: I - Tree water status. Environmental and Experimental Botany, Volume 152:107-117
https://doi.org/10.1016/j.envexpbot.2018.01.002

Förster, L.; Trauner, A.; Eberl, V.; Brunner, S.; **Neumann, L.**; Sauer, B.; Fritz, M. (2019): Amarant als Biogassubstrat-Selektion zur Erarbeitung praxistauglicher Amarantlinien für bayerische Standorte. Berichte aus dem TFZ 64; ISSN: 1614-1008; Hrsg.: Technologie-und Förderzentrum im Kompetenzzentrum für Nachwachsende Rohstoffe (TFZ) Schulgasse 18, 94315 Straubing